SOCIO-ECOLOGY OF NON-BREEDING CHOUGHS

Pyrrhocorax pyrrhocorax

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I declare that this thesis, composed by myself, has not been accepted in any previous application for a degree. All sources of reference and quotation have been duly acknowledged.

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SUMMARY

Observations of colour-ringed choughs were carried out at communal roosts and feeding flocks.

1. Of the three roosts studied, one was in continual use over the whole year holding from 30 to 120 choughs. The other two roosts were used by family groups after fledging and by young birds over the late autumn and were not in use all year.

2. The numbers of choughs using communal roosts were not static. The highest numbers were during the summer period when the young were fledging.

3. At the roost which was in continual use, numbers of first and second year choughs fluctuated to a greater degree than those of older birds with young birds moving to other roosts during the autumn / winter.

4. At the roost which was in continual use and where detailed observation of individual choughs could be carried out, there was an age-related dominance hierarchy with older birds winning and initiating more aggressive interactions than young birds (particularly first years). The majority of aggressive interactions were settled by threat rather than physical contact.

5. Young choughs arrived in the evening at the communal roost earlier and were less site-faithful in their roosting positions than older birds.

6. There was segregation of age classes within the roost flock during the summer with second nearest neighbours of each age class being of the same age greater than expected by chance. There was no difference from random in the age associations during the winter.

7. Choughs arrived earlier in the evening and at higher light intensities during the summer months than in the winter. The time at which birds arrived at the roost was more closely associated with time before sunset than light intensity. However,

settling in the roost was more closely associated with light intensity than time before sunset.

8. Experimental food patches were provided on six occasions during the winter to test the "information centre" hypothesis. Choughs took several hours after dawn to find the bait on the first day but were quick to return after leaving the roost the following day (i.e. within minutes). More birds arrived on the second day. The reason for this is unknown but may be due to birds following others out from the roost, or local enhancement. The fact that choughs quickly returned to the experimental food patch suggests that they are quick to take advantage of newly avaiable food sources especially during the winter.

9. Set route surveys were carried out and the locations of colour-ringed choughs recorded. The areas in which 75% of roosting choughs were found feeding from each roost did not overlap though these discrete "core " areas were not defended.

10. Foraging range from the roost varied seasonally with birds foraging further in the summer. Young choughs foraged further (nearly twice as far) during the winter than older birds.

11. There was no significant difference in the distribution of flock sizes between seasons although in spring and summer the highest proportion of flock sizes being flocks of two.

12. There were differences in the proportions of different age classes in different areas. There were also differences in the proportions of different age classes depending on flock size. In an area where a higher proportion of the population was composed of older choughs, first year choughs tended to be found in smaller flocks especially during the winter. In areas where there were few older choughs present, first year choughs tended to flock together and were found in higher proportions in larger flocks than in an area where there were more older birds.

13. In feeding flocks individual birds' vigilance was related to flock size, decreasing with increasing flock size. For first year choughs however, as flock size increased

over 11-15, their vigilance levels increased. This was possibly related to aggression avoidance when feeding on patchy, defendable food such as cow dung, or may have been related to observational learning when feeding on cryptic, non-defendable food items such as sub-soil invertebrates. As flock size increase, rates of aggressive interactions increased especially when choughs were feeding on dung and involved first year choughs to a greater extent than older birds.

14. Young choughs with their parents, while feeding on food items within dung had higher feeding rates, spent more time feeding and less time begging than when the family group was feeding on subsoil invertebrates.

15. Although sample size was small, the majority of colour-ringed female first time breeders were three, although several did breed in their second year. A higher proportion of first time breeders of four years old or over were male.

CONTENTS

1. INTRODUCTION

1.1 DEFERRED BREEDING

Deferred breeding or delayed maturity in birds can be the result of several factors. A lack of suitable nest sites and territories may force birds which are relatively sedentary to wait until such breeding sites or territories are available before they can breed, (Brown 1969).

The type of food taken by birds may also play a part. If food is difficult to find (cryptic or scarce) or difficult to handle, then young birds may have to go through a period of learning (Shettleworth 1972, Richardson & Verbeek 1987, Walker 1987, Marchetti & Price 1989) before they are capable of maintaining not only themselves but also dependent young, (Davies & Green 1976, Maclean 1986, Richardson & Verbeek 1987). Time must therefore be spent in developing these feeding skills before the bird is capable of reaching the body condition necessary to breed and feed young.

In some species, deferred breeding can be seen in more complex associations based on the extended family unit with deferred breeders helping at the nests of relatives, (Fry 1972, Woolfenden 1975, Rowley 1978, Brown & Brown 1982).

Delayed maturity or deferred breeding may result in the development of complex social organisations. Non- breeding birds may flock, foraging and roosting together, (Charles 1972, Smith 1978), lead a solitary existence or remain on their territories. Within a species, several strategies may be employed such as in the Magpie (*Pica pica*) where young non-breeders may join flocks or remain within their parent's territory, (Eden 1989).

Where the identification of individuals is possible, a clearer picture of the social behaviour of that species can be formed. Breeders can be distinguished from non-breeders, different age classes may be identifiable, and the social organisation and demographic structure of the population investigated. Within the non-breeding population, social behaviour can be studied to give insights into the advantages and disadvantages of flocking, and the relevant strategies used and choices made by individuals which may increase their chances of breeding in the future.

1.2. THE STUDY SPECIES

1.2.1 DESCRIPTION

The chough *Pyrrhocorax pyrrhocorax* is a member of the Corvidae, the rarest of its family in Britain. It is a distinctive bird, the adult with glossy blue-black body plumage and glossy black-green wings. The long, slightly decurved bill and the legs are bright red although fading can occur. Juveniles before their first moult have browner plumage and after fledging the bill and legs are a more orange/yellow than adults (Goodwin 1976). In body size they are between jackdaws (*Corvus monedula*) and crows (*Corvus corone*), with a body length of between 36 and 41 cm, somewhat more slender. Males are slightly larger in body weight than females with greater wing bill and leg length, although difficult to tell apart in the field for the first year at least. Two of the most distinctive features of this bird at a distance are its buoyant acrobatic flight often with primary feathers separated, and its most predominant loud, far-carrying vocalisation which maybe gave the bird its onomatopoeic name which originally may have been pronounced "chow" rather than "chuff".

1.2.2 DISTRIBUTION

The chough is widely but discontinuously distributed across southern Europe eastwards through Turkey and the Middle East to the USSR, Himalayas, China and Mongolia. There is also an isolated population in northern Ethiopia. In continental Europe it has outposts in Brittany and the Canary Islands (on Palma only). Figure 1.2.1. shows the world distribution.

In Britain (Figure 1.2.2) populations occur in Wales, the Isle of Man, and in Scotland where the largest numbers occur on the islands of Islay and Colonsay, both in the Inner Hebrides. Several pairs also occur on Jura and, until recently, choughs bred on the Mull of Kintyre. The British and Irish survey conducted in 1982 found that Ireland contained 72% of the total population (656-685 breeding pairs and 615-623 non-breeding individuals), Wales contained 16% (139-142 breeding pairs and 103-106 non-breeding individuals), the Isle of Man contained 6% (49-60 breeding pairs and 61-65 nonbreeding individuals) and Islay also contained 6% (53-61 breeding pairs with a non-breeding population of 32-50 individuals), Bullock *et al.* (1983a). No recent national survey has been carried out so current numbers are unknown. There is a distinctly restricted westerly distribution, the reasons for which are not well understood although food availability and climate may be important.

1.2.3 FOOD AND FEEDING HABITATS.

The most distinct feature of the chough which separates it from other British corvids is its strong curved bill which it uses to dig and probe for food. A number of studies have now confirmed the choughs general diet (Cowdy 1973, Bullock 1980, Roberts 1982 and Warnes 1983a). Almost exclusively, the chough feeds on insects in particular soil-living invertebrate larvae especially leatherjackets (*Tipula* spp.),

FIGURE 1.2.1

World distribution of the chough *Pyrrhocorax pyrrhocorax*.

(after Goodwin 1976).

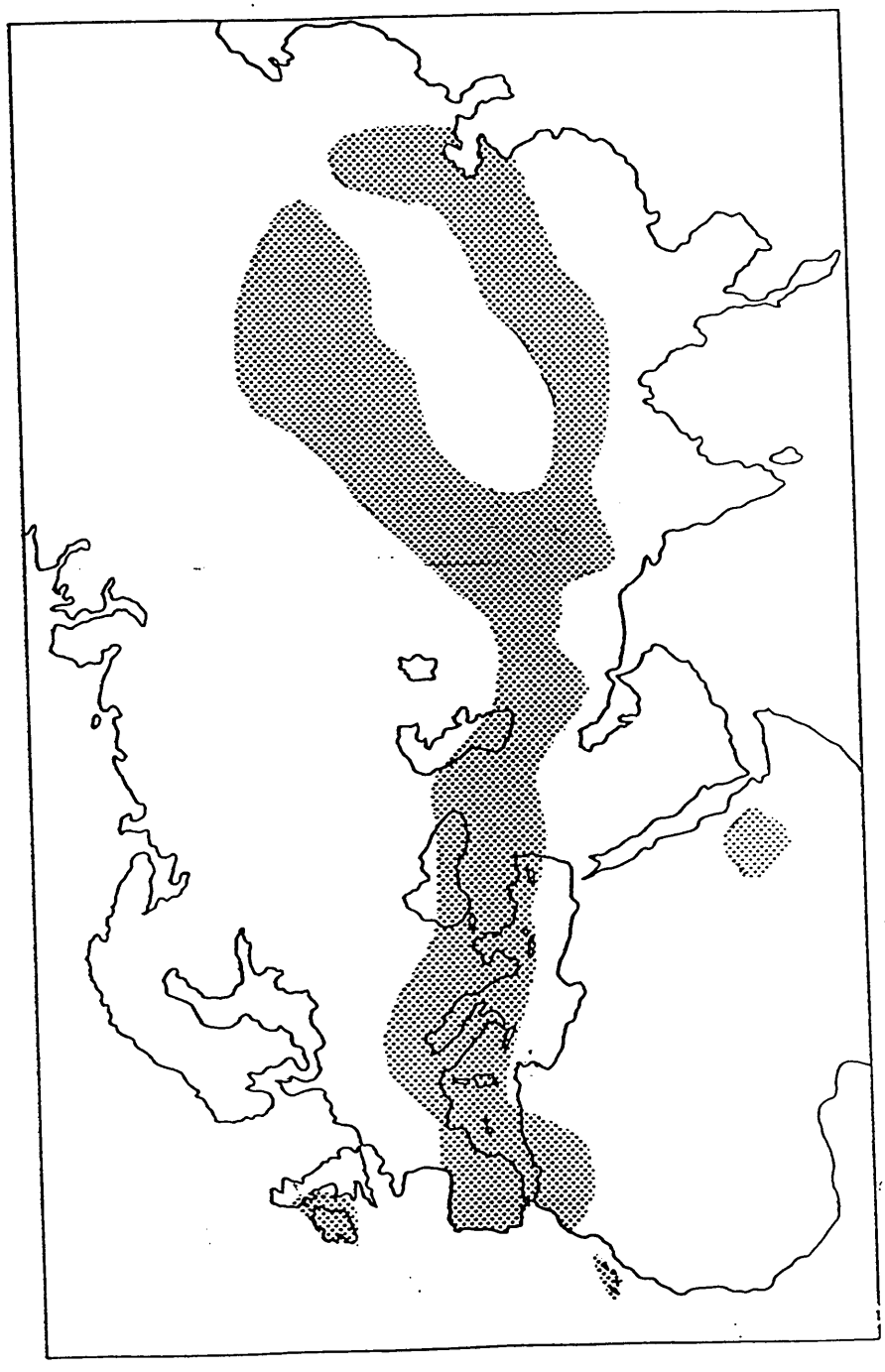


FIGURE 1.2.2

Breeding range of the chough in Britain and Ireland. (after Sharrock 1976).

beetle and moth larvae. Another food source has been found to be ants (Cowdy 1973). Dung beetles (Scarabids) and their larvae within and under cow, horse and sheep dung are another important source of food. The availability of the above food types however may vary from area to area within the choughs' range. Bullock (1980) suggested that food availability alone within the soil is not the factor which restricts the range of the chough. Rather it is the access to this food which is important. For choughs to be able to feed on sub-soil food, the vegetation levels must be short enough to allow access to the soil by digging. This short vegetation is predominately associated with maritime heath which is occasionally burned (Haycock & Bullock 1982), maritime turf or short- grazed traditional pastures. Improved grazing which has not been disturbed by long-term ploughing may also yield high concentrations of sub-soil invertebrates. On Islay, newly cut silage and hay fields provide choughs with good feeding habitat (pers. obs.) Stubble fields in the autumn and winter also provide spilled grain which choughs will readily use. Choughs in other parts of its British and Irish range have been observed regularly feeding on beaches (Roberts 1982 & 1983) especially in the winter when seaweed accumulates after storms and sandhoppers, (*Orchestia gammarella*) and the larvae of the kelp fly (*Coelopa frigida*) are available. From observation of choughs on Islay, beach feeding does not seem to occur to the same extent as it does in other areas such as on Bardsey Island off the north-west coast of Wales, and on the Isle of Man and Ireland.

The climate on the west coast of the British Isles is milder than inland with warmer winters which usually guarantees freedom from frost and snow thus allowing the chough access to sub-soil food at all times. The milder winters may also sustain greater insect activity (Bullock *et al.* 1983a)

1.2.4 THE CHOUGH ON ISLAY: NUMBERS AND PROPORTION OF NON-BREEDERS.

This study was carried out on the Isle of Islay in the Inner Hebrides where in 1982, 6% of the choughs in Britain and Ireland were found. (Bullock *et al.* 1983a). Islay is the stronghold of the chough in Scotland containing 90% of the total Scottish population (Monaghan *et al.* 1989).

There are few data on the age of first breeding although Holyoak (1972) suggested an age of three years on the assumption that the chough was similar to other better studied corvids. Roberts (1985) found that many choughs on Bardsey did not breed until four years old and that this may reflect a dense population on a relatively small island. Young choughs may be unable to compete for limited nest sites and territories. This may result in delayed breeding and perhaps greater dispersal than is seen in areas with a lower population density. Bullock *et al.* (1983a) suggested an age of first breeding of three or older. From the little available data there is obviously a large proportion of the non-breeding population older than one year old. On Islay, birds of five had yet to breed (pers obs.).

There have been various estimates of the proportions of non-breeding choughs in British populations. These estimates have come from surveys carried out during the breeding season when breeders have been assumed to be on their territories. Therefore flocks of choughs and pairs not holding territories were assumed to be non-breeders. The Scottish survey carried out in 1986 may have been more accurate than other surveys as colour-ringed choughs made possible individual recognition and therefore the status of birds as breeders or non-breeders more certain. During the Scottish survey in 1986, 86 breeding pairs were confirmed on Islay (172 birds) with a non-breeding population of between 90 and 100, (Monaghan

et al. 1989). Thus 34 - 36% of the Islay population was composed of non-breeding birds. This is similar to the overall British and Irish survey in 1982 (Bullock *et al.* 1983a) where 31-32% of the total population consisted of non-breeders. Rolfe (1966) suggested a non-breeding population of 30% for Britain and Ireland. Bullock *et al.* (1983b) found a non-breeding population of 32% in Ireland. These are remarkably similar figures which do not seem to have changed much since Rolfe's estimate of 1963 (Rolfe 1966) although Holyoak (1972), using observations for several locations particularly the Isle of Man and Wales, suggested that the level may be higher. From Warnes (1983b) a proportion of non-breeders of 23-29% on Islay can be calculated for 1982 which is slightly lower than the 1986 survey. This may be due to poorer coverage in finding non-breeding flocks but may also be due to a genuine increase in the non-breeding proportion within the population. Roberts (1985) found the non-breeding proportion of the population on Bardsey Island, Wales to vary from 20-60% between 1953 - 1983. Thus overall, the non-breeding proportion in British Isles chough populations is generally between 20-40%.

1.2.5 THE HISTORY OF THE CHOUGH ON ISLAY AND THE REST OF SCOTLAND

Baxter & Rintoul (1953) gathered together records on the changing chough population in Scotland. During the 19th Century it appears that the chough was widely distributed on coasts and in both lowland and highland areas. Around the 1830's they had died out inland but on the coasts they survived for longer. Buchanan (1882) stated that there had been a decline in choughs on the east coast of Scotland since the early 1800's although it has never been clear if there were significant numbers originally. He also stated that Islay contained the highest numbers in Scotland and that from recent accounts of that time, the population did

not appear to be diminishing. The decline of the chough on the west coast came later and by the start of the 20th century they were only found on Islay, Jura, Mull of Kintyre, Ayrshire and Wigtownshire.

In the 1960's the population on Islay was estimated at 135-140 birds (Booth & Taylor unpub. in Warnes 1983b). The nearby island of Colonsay used to contain large numbers but by 1980 only one pair was found (Warnes 1983b). Since then the population has expanded again with 6 pairs and a non-breeding population of 10 (Monaghan *et al.* 1989).

As two choughs breeding on Colonsay were colour-ringed on Islay, it seems that emigration from Islay may have allowed the re-expansion of the Colonsay population. Colour-ringed birds have also been sighted elsewhere: there are tentative sightings of a colour-ringed bird on Tiree and confirmed sightings of colour-ringed birds on Jura. There are also reports of pairs or single unringed birds visiting Mull and Iona and a sighting on the Gravellichs an island group to the north-east of Jura (M. Muir pers. comm.). From this it seems that the population may now be expanding its range. As birds are moving from Islay, it is possible that there is a limiting factor in nest site and territory availability which means that birds which do not leave the island may have to delay breeding.

1.2.6 PREVIOUS STUDIES

The majority of literature on the chough deals with breeding success and survival (Rolfe 1966, Bullock *et al.* 1983a, Roberts 1985, Bignal *et al.* 1987), distribution and status, (Bullock *et al.* 1983a & b, Warnes 1983b, Monaghan *et al.* 1989) or with feeding ecology, (Holyoak 1967, Bullock 1980, Roberts 1982 & 1983, Warnes 1983a) with little on flocking behaviour (Lovari 1976, 1978). There has been very little

work on the social behaviour of choughs other than flocking and practically nothing is known about the non-breeders in the population. It is these birds which become the future breeders and as such attention must be directed to them as well as to the breeding birds. Without a healthy pool of non-breeders, the attention paid to breeding birds' conservation would be fairly pointless since populations will decline through lack of recruitment.

1.2.7 OUTLINE OF THESIS

With a population of ringed choughs of known age and individually identifiable which has been established on Islay (see Methods), it is possible to investigate the behaviour and social structure of this non-breeding segment of the population.

In this study flock structure and behaviour, roosting behaviour and movements of non-breeding birds will be investigated in relation to social behaviour. Age of first breeding will also be examined. No attempt has been made to deal with habitat use and food requirements as this in itself would require an individual study. Much previous work has been concentrated on feeding habitats and food requirements (see above) and more is currently being carried out, although concentrated on breeding birds during and outwith the breeding season.

Non-breeding choughs are defined as birds which have never bred, and data were collected on these birds when they were either roosting communally or flocking. Choughs which have held territories but not bred, and subsequently returned to the non-breeding flocks, are included with non-breeders. No data were collected on pairs of birds on their territories whether breeding or just holding territories. Breeding birds which have returned to the non-breeding flocks with fledged young are not included.

2. METHODS

2.1. THE STUDY SITE

The location of this study was the Isle of Islay, a member of the Inner Hebrides group off the west coast of Scotland at long.6"15'W lat.55"50'N, (Figure 2.1). The island covers an area of just over 600 km^2 and measures approximately 25km wide by 40km long.

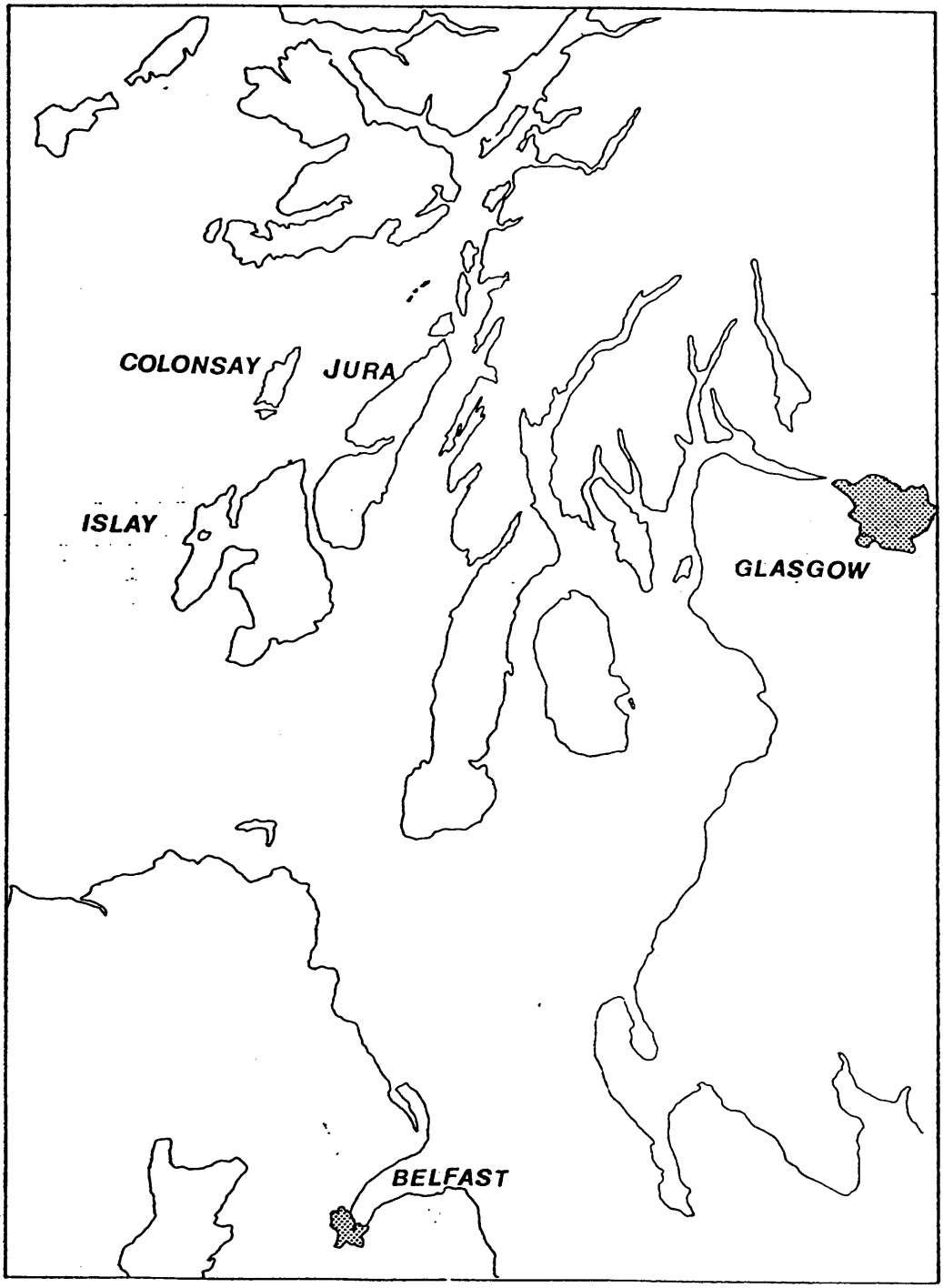
The island has a wide variety of habitats ranging from woodland and lush agricultural land on limestone to montane areas on igneous rock in the south east. There are large tracts of moorland and rough grazing and areas of dunes and dune pasture mostly on the western seaboard. Compared to much of mainland Scotland, the winter is mild and the summers tend to be warm and wet.

2.2. COLOUR RINGING

An intensive colour-ringing scheme has been in operation since 1983 with young birds marked while still in the nest. Each nestling was ringed with a year specific colour-ring on one leg with most also having a B.T.O. ring below. The other leg carried an individual two colour-ring combination allowing each bird to be individually recognisable in the field. As colour- ringing progressed, nine colours were eventually used thus allowing 81 individual combinations to be used in any one year. As the year-specific colour was changed each year, this meant that the same two colour-ring combination on the other leg could be used again during the following years. If more than 81 nestlings were colour-ringed in any one year, an individual two ring combination was used without a year code. This meant that the combination could not then be repeated.

FIGURE 2.1

The location of the study area, the Isle of Islay in the Inner Hebrides. The islands of Jura and Colonsay which have small populations of choughs are also shown.


COLONSAY
JURA
ISLAY
GLASGOW
BELFAST

2.3. OBSERVATIONS

2.3.1 GENERAL OBSERVATIONS

Choughs were observed using a variable power telescope (20-60X magnification) and 10 X 50 binoculars. Birds were observed from as far away as practicable so that they were not disturbed by human presence but at a distance where detailed observations could still be made and individuals identified. This distance varied depending on the amount of intervening cover. However, it was often possible to approach quite close (20m) from behind walls and sand dunes. At other times, especially in open habitat birds had to be observed from distances from 300 to 600m. Observations were made from a vehicle used as a "mobile hide" as well as on foot. To obtain sufficient data on colour-ringed choughs, areas were visited where choughs were known to be present on a regular basis. However, no effort was therefore made to randomise site visits and each feeding area received approximately equal coverage. Other outlying areas were also visited regularly to pick up any movement of birds.

When a flock was encountered all colour-ringed birds were recorded if possible. Flocksize, date, time, grid reference, habitat and food items taken (if possible) were also recorded.

If the flock remained in the same location and habitat for longer than 30 minutes the same observations were re-recorded. This was an arbitrary time interval used to investigate associations between birds as flocks often did not stay together or in the same location for long periods. . At any change of flocksize, flock composition or location, a new observation was recorded. However, the larger the flock, the longer the time it took to record the identities of marked birds. If observations on a large flock took longer than 30 minutes and the flock had remained constant over that time then a second record of the flock could be made into the second 30 minute period. This seldom occurred as it was difficult to keep track of all individuals

within the flock. Usually this only happened when the flock was in an open habitat with all birds clearly in view and where movements to and from the flock would have been clearly observable. The flock would be scanned twice if possible and a double-check made on the identities of individuals for all observations.

2.3.2 DIFFICULTIES IN OBSERVATION AND RECOMMENDATIONS ON THE USE OF COLOUR-RINGS.

Several factors influenced the ability to identify colour-ringed birds such as the length of grass or stubble or rapid movement of the bird. The distance from which observations could be made depended on such things as wind speed (causing telescope shake), light intensity (if too bright causing glare on the colour rings) and heat haze which proved to be a major problem in the summer months. The actual colours themselves proved different in their ease of recognition if conditions were poor i.e. some colours were more difficult to identify than others. In fact certain combinations of colours proved more difficult than others to identify due to the effect one colour had upon another.

A trial was conducted whereby colour-rings were placed on thin strips of red-painted wood to imitate choughs' legs. Combinations of colour-rings not known to me were then set out by an assistant in an area of open dune pasture at varying distances and in good conditions (calm, bright overcast with no heat haze) and repeated when there was a heat haze and when light intensities were low. It is pertinent to make some recommendations for future work using colour-ringing based on the results of this trial and general field observations.

i) Bright colours such as red, yellow and orange were easily identifiable in all conditions (and at the greatest distances 650-700m in good conditions.

ii) The colours blue and green become more difficult to identify accurately at distance and the problem was exacerbated by low light or heat haze.

iii) Lime coloured rings were confused with white at a distance and in poor light. White could be confused with lime when the white became worn or when birds were being observed at roost in the orange/yellow evening light when the sun was setting.

iv) The most difficult ring colour to identify (under all conditions) was grey. This could easily be confused with blue and, if the other colour in the combination was blue or green, tended to pick up that colour.

If one recommendation had to be made about the use of colour-rings in any accurate, future intensive study I would strongly recommend the restriction on the use of grey colour-rings especially in combination with blue or green. However, as one who has spent nearly four years regularly identifying colour-rings, these problems may be more acute for a new observer as there is definitely a period of improvement in ring-reading ability. For this reason casual observations from others were never used in any of the following studies except from other people regularly observing choughs and even then only at nest sites where close observations were possible.

2.3.3 SPECIFIC OBSERVATIONS

Much of the data collected for this study was in the form of specific observations. Three types of recording took place: Roost observations, surveys, and activity budgets. These are dealt with in the relevant section's methods.

It was impossible to examine behaviour in relation to sex as young choughs are difficult to sex accurately in the field. It is not until birds are older that sexing is possible at nest sites where the female alone incubates. (Goodwin 1976).

2.3.4 MAIN STUDY SITES

The majority of observations were centred in areas where non-breeding birds were known to be regularly found (Figure 2.2), although visits to other areas were also made on a regular basis. Observations were also recorded at nest sites along with colour-ring sightings by other experienced workers to pick up birds which had moved from the non-breeding flocks to breed or visit territories.

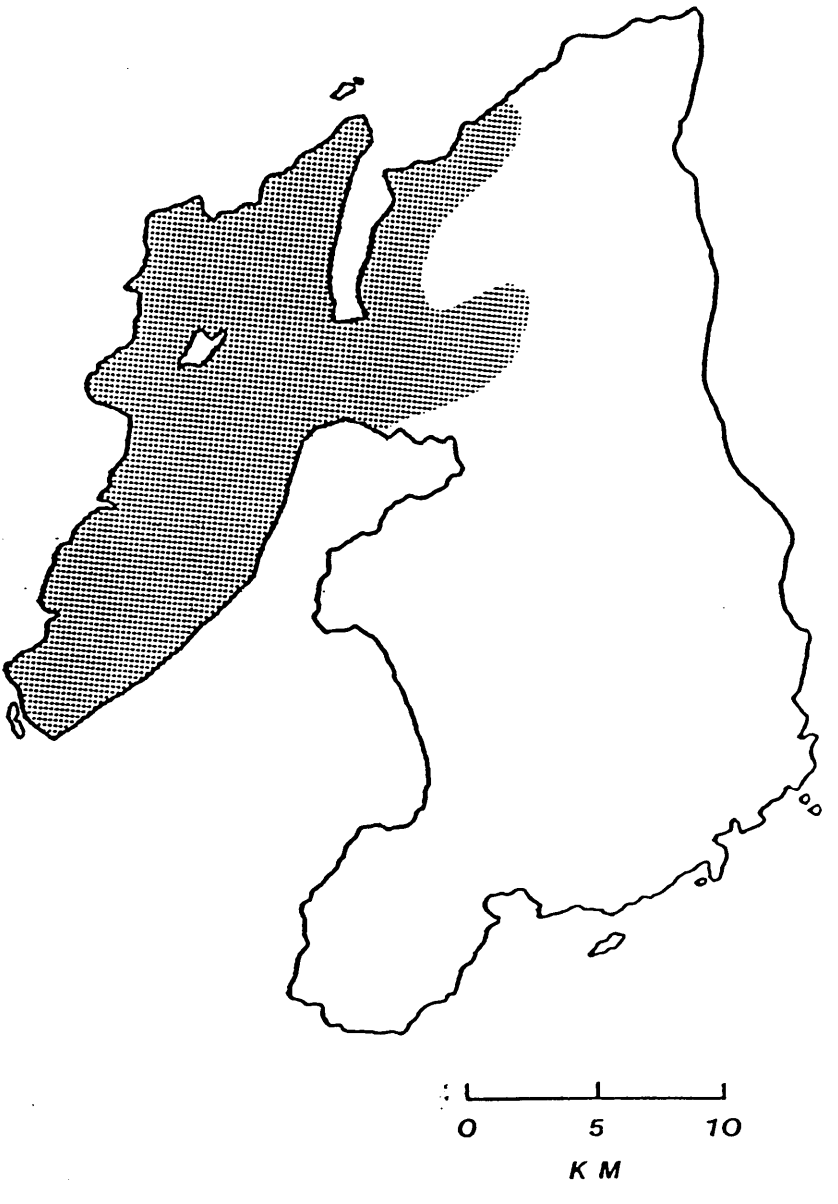
The roost site at which most of the observations on roosting behaviour were made was at Kilchoman (Roost 1) situated in the north west of the island. This roost was a traditional site which was used on a regular basis and by the largest numbers of non-breeding choughs over the whole year. Breeding choughs also attended the roost with their young after fledging, returning to their territories after their young were independant. Failed breeders often returned to the roost as did birds which were holding territories although not breeding.

The birds roosted on a sheer vertical cliff on the WSW side of a large inland gully 1.2 km from the sea to the west and sheltered from the prevailing westerly winds. The cliff measured approximately 21 m high and choughs roosted in abundant crevices, on ledges and in small areas of vegetation. The area used by the majority of choughs measured 80-100 m^2 with only small numbers roosting in other parts and on the opposite side of the gully. The cliff was also used by several pairs of breeding fulmars *Fulmarus glacialis*, roosting jackdaws *Corvus monedula* and roosting starlings *Sturnus vulgaris*. Observations were made using 10 X 50 binoculars, 15 m from the base of the roost cliff. The birds appeared undisturbed by human presence at the roost as long as movements and sound were kept to a minimum. The positions of colour-ringed birds were marked onto a photocopied composite photograph of the cliff face (scale 1cm = 1m). Details of observations can be found in the relevant section's methods.

Two further roosts were regularly monitored to pick up the movements of birds to

FIGURE 2.2

The main study area on Islay (shown by shading) where the majority of fieldwork was undertaken.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and from roosts. Roost 2 was situated near Killinallan in the north west of the island on a low inland, westerly facing gully. Observations of colour-ringed birds were restricted by the roosting positions of the choughs. No data other than colour-ring sightings could be collected as it was impossible to observe the choughs after they had settled on the cliff face to roost. This roost was not in use over the whole year, in general only by family parties after fledging in July until spring when birds moved to other locations. The third roost (Roost 3) which was monitored was located in the north east of the island although the actual location moved several hundred meters between sites. This, like Roost 2, was not in continual use over the whole year. Here too, the majority of birds using this roost were family groups after fledging in July, over the winter period and into the late spring. The actual roost location was occasionally on an inland cliff and at other times the birds moved to a cliff above the sea. Here too (as in Roost 2), observations on roosting birds were restricted to colour-ring sightings.

2.4 CLASSIFICATION OF FIRST YEAR CHOUGHS

The date on which fledged choughs were first sighted at the roost in 1985 was the 1st July and in 1986 and 1987 the first sighting was the 4th July on both occasions. Thus, choughs were classed as first years until the following 1st of July, when the next year's young were fledged and first sighted at the communal roost. After this date the previous year's cohort was classed as second years. This classification was also used in data collected on feeding flocks as no newly fledged choughs were seen in non-breeding flocks before the 1st of July.

2.5 DATA STORAGE AND STATISTICAL ANALYSIS

Data were recorded in field notebooks and also on a hand held tape recorder. All observations were later transferred to a computer database (DBase II (C) Ashton-Tate). Data were analysed using Statpack (C) Northwest Analytical, Inc. and SPSS/PC+. Specialist analyses programs were written in FORTRAN by M. Still. Statistical analyses followed Sokal & Rohlf (1969) and Ripley (1981).

3. ROOSTING BEHAVIOUR

3.1. CHAPTER INTRODUCTION.

Communal roosting in birds is likely to have adaptive significance, which may relate to anti-predator, social or foraging advantages, (Ward 1965, Lack 1968, Bertram 1978, Ward & Zahavi 1973).

In this chapter fluctuations in numbers of choughs using the largest regular communal roost at Kilchoman, (Roost 1), are investigated over the study period, and details of age differences in roost attendance are examined. To do this, detailed observations on arrivals and departures from the roost were related to the movement of birds to and from roosts in other feeding areas, and the movement of birds in relation to breeding status. Thus fluctuations in numbers can be equated with age differences in the behaviour of birds using the roost. Sections within this chapter will have their own introduction, methods and results where appropriate.

The use of the communal roost as an "information centre", as proposed by Ward & Zahavi (1973) and Weatherhead (1983), was examined on an experimental basis. Roosting behaviour in relation to environmental conditions (day length and light intensity) were also examined.

3.2. ROOST DYNAMICS.

3.2.1 INTRODUCTION.

Both short term and seasonal variations in the numbers of birds using a communal night roost are likely to reflect variations in the foraging behaviour and location of such birds.

Variations in the numbers of birds using a particular communal roost have been noted for pied wagtails, *Motacilla alba*, (Fleming 1980) where numbers varied at a roost from two to an estimated 1215. Roost numbers changed with changes in the feeding locations used, with birds using alternative roosts in harsh weather. Brodie (1976) found that numbers of starlings (*Sturnus vulgaris*) using a communal roost fluctuated during the year with the largest numbers present during the winter. Buitron (1983) found that after fledging, young magpies (*Pica pica*) started to associate with birds from other broods after about six weeks although some remained solitary. These non- breeding magpies flocked loosely and roost numbers varied between 10 and 52 with a peak in January and February.

The variations in numbers of different ages of birds using a roost may reflect age related differences in behaviour of the birds; to study this, one must be able to recognise different age classes in the field. The use of colour-ringed birds of known age allows the identification of different cohorts within the population. If these colour-ringed birds are assumed to be representative of their cohorts, then the study of these colour-ringed birds can give some indication of the behaviour of their respective age-classes as a whole.

The objectives of this section were to examine seasonal changes in roost attendance and age composition of choughs using Roost 1. (This roost was in constant use over the whole year). For the purposes of future surveys to ascertain the status and age composition of the chough population, counts carried out at roosts must take into account any seasonal differences if an accurate conclusion is to be drawn from roost counts.

3.2.1 METHODS.

A total of 271 nightly visits were made to the communal roost at Kilchoman, (Roost 1), where the majority of studies of chough roosting behaviour took place. These visits were made between 5/3/85 and 8/2/88 and a total of 8054 sightings of colour-ringed choughs were made at this roost between these dates. Counts of all choughs, both colour-ringed and unringed, were made on each nightly visit. This could be achieved as birds entered the roost in small groups or during pre-roost gatherings which sometimes occurred, either in an open field directly below the roost cliff or on open moorland above. Birds could also be counted in pre-roost communal flights around and above the roost. If, as sometimes occurred, birds arrived at the roost in one large flock and settled directly on the cliff face, numbers had to be counted actually within the roost. This was possibly less accurate than counts made in a pre-roost flock as birds often settled into cracks and behind vegetation relatively soon after arrival. This made counting more difficult as birds could be easily overlooked.

The mean number of colour-ringed choughs in each age class present at the roost was calculated for each month. As choughs were ringed as chicks each year and the sightings of choughs covered more than one year, it was possible to examine the behaviour of a particular age class based on data from more than one cohort.

To calculate the age structure of the population of choughs using the roost, it is necessary to take into account differences in the proportion of fledged choughs using the roost which were actually ringed each year since ringing effort varied between years. For this it is necessary to know the numbers of ringed young which fledged each year, and the total number of fledged young: the latter was estimated from the number of breeding pairs and the mean fledging success. To calculate the number of breeding pairs which produce young which subsequently use this communal roost, the areas from which colour-ringed choughs have come to the Roost 1 in their first year from between 1985 and 1987 were plotted (Figure 3.2.1).

The majority of ringing has taken place on the Rhinns and "Elsewhere" areas and numerically the largest number of fledged choughs sighted at the roost have come from this area too. Only one chough from the Oa area was seen at Roost 1 in its first year, although numbers ringed are too small to give an accurate insight into the movements of birds from this area to the roost. The few birds in the Oa area which arrived at the roost did so much later in the year than young ringed on the Rhinns and "Elsewhere" and thus birds from the Oa area did not seem to frequent the roost at Kilchoman (Roost 1) to any great extent. Using this as a guide and thereby excluding the Oa area, the number of breeding pairs used in the calculation of corrected numbers was set as the number present on the Rhinns and "Elsewhere". The number of breeding pairs was taken as 63 for this area over the period of the study from a survey carried out in 1986, (Monaghan *et al.* 1989).

The mean fledging success over a three year period on Islay was calculated as 2.02 young per nest (Bignal *et al.* 1987). It has been assumed that, for the purposes of this calculation, there was no significant difference in fledging success from year to year as there are no complete data available sufficient to say otherwise. The data for the numbers of fledged colour-ringed young each year are a result of a fairly widespread coverage of nests at, or soon after fledging, by myself and others although it was impossible to cover the whole island completely in such a short time. Therefore, the numbers of colour-ringed fledged young must be taken as the minimum. The calculation used to determine the proportion of a cohort which was colour-ringed equals:-

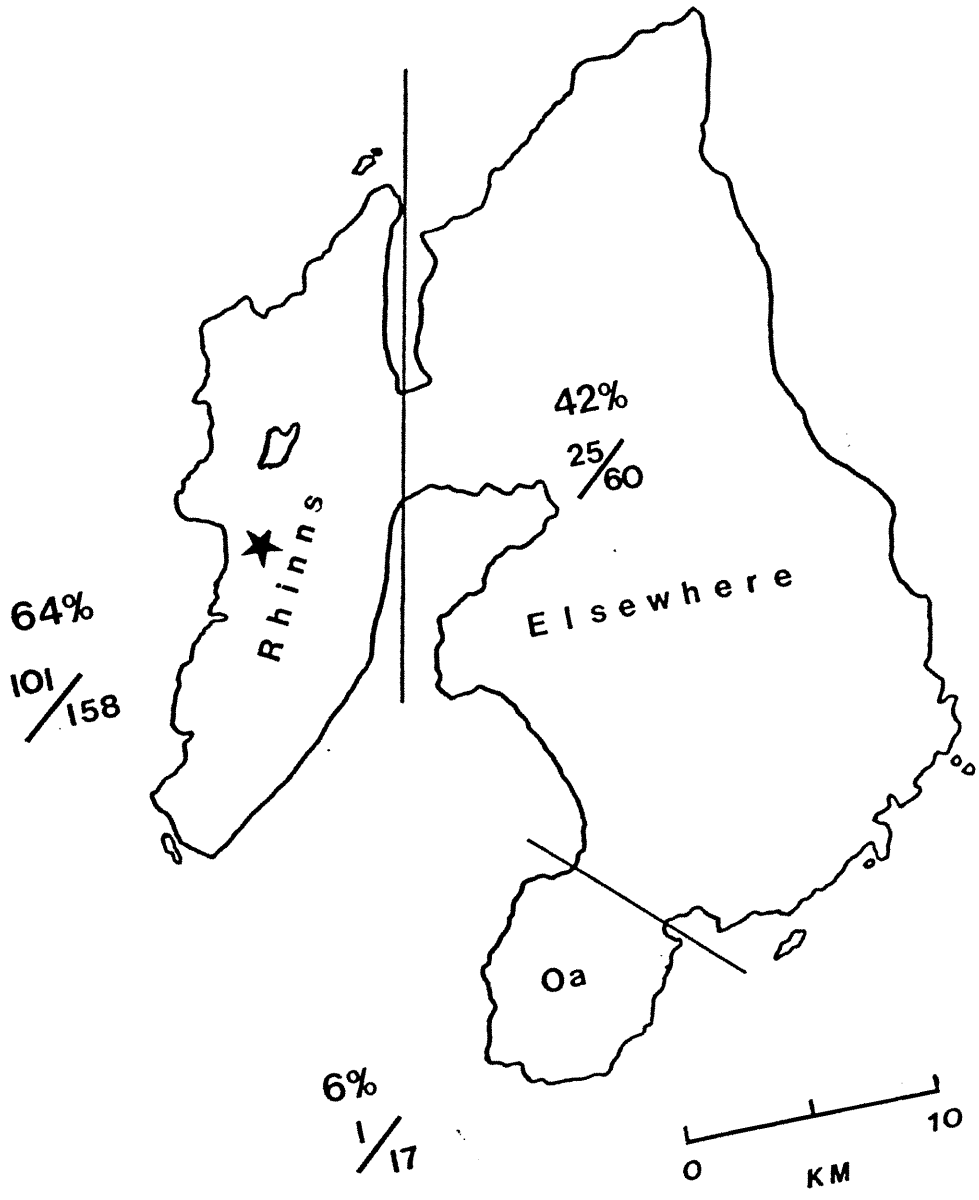
$$\frac{\text{The number of fledged colour-ringed choughs}}{\text{The number of nests (63)} \times \text{The mean fledging success (2.02)}}$$

Table 3.2.1. shows the results of this calculation.

FIGURE 3.2.1

Map of Islay defining the three areas: Rhinns, "Elsewhere" and Oa with the percentage of all the colour- ringed choughs which were ringed in each area and subsequently were sighted at the main study roost (Roost 1) in their first year. The data are for choughs ringed in the nest between 1985 and 1987.

Roost 1 is depicted by a star.


42%
25/60
Rhinns
Elsewhere
64%
101/158
Oa
6%
1/17
0
10
KM

3.2.2 RESULTS.

Figure 3.2.2 shows the mean monthly numbers of choughs (both marked and unmarked) present at the roost during the study period. The full data (means $\pm$ 1 s.e) are in Appendix 1. These data show that there has been an overall decrease in the numbers of choughs using the roost over the study period. Within this pattern of decrease however, there are fluctuations in numbers. These fluctuations in numbers seem to show a pattern and are not purely random. Increases in numbers occur in July and August along with a peak in numbers in late winter/early spring in 1985/1986. Figures 3.2.3 and 3.2.4 show the annual variation in age composition of the roost based on the mean monthly numbers of each age class present at the roost, combined for all years and corrected for differences in the proportion of each cohort ringed as shown in Table 3.2.1.

For all age classes, the numbers of choughs using the roost during the autumn and winter months decreased although this pattern is not as marked for 4th and 5th year choughs (Figure 3.2.4). Numbers tended to rise again in the spring with a peak in numbers in July/August for all ages except fourth years. A correlation was found between the number of first and the number of second year choughs at the roost at the same time ($r_S = 0.745$, N=11, $p < 0.01$), (Figure 3.2.3), and also a correlation between third and fourth years ($r_S = 0.70$, N=11, $p < 0.05$). There were no significant correlations between any other ages classes of choughs present at the roost.

Annual differences in the pattern of seasonal variations in numbers within an age-class i.e. between cohorts at the same age was also examined. Figures 3.2.5 to 3.2.8 show the mean monthly numbers of each age class present corrected for the proportion of that cohort colour-ringed (Table 3.2.1.). Each of these figures (Figures

3.2.5 to 3.2.8) shows the data available for numbers of each cohort at the same comparable age. Using cohorts for which there was for more than seven corresponding months' data, the mean degree of association between years in monthly roost numbers were analysed using Spearman Rank correlation. The results are shown in Table 3.2.2.

The only two cohorts which show any significant correlation between years were cohorts in their 3rd year. These data suggest that while the pattern of roost use can differ between years for birds of the same age the overall pattern of use between different cohorts at the same age was broadly similar only for third year birds

TABLE 3.2.1. Calculated proportion of colour-ringed choughs in each cohort based on 63 breeding pairs and mean fledging success of 2.02.

YEAR	NO. FLEDGED COLOUR-RINGED YOUNG	PROPORTION COLOUR-RINGED IN COHORT
1983	40	0.31
1984	49	0.38
1985	80	0.63
1986	53	0.42
1987	63	0.49

Table 3.2.2.. Mean monthly corrected roost numbers of different cohorts at the same comparable age. (Correlations only between cohorts with more than seven corresponding months data.)

	1st Year Age-class.		2nd Year Age-class.		3rd Year Age-class.	
MONTH	Cohort 1985	vs.1986	Cohort 1984	vs.1985	Cohort 1983	vs.1984
JUL	16.2	7.0	51.2	20.3	30.4	33.0
SEP	13.6	24.2	34.1	14.2	24.6	26.3
JAN	6.4	0.0	18.2	6.4	22.4	22.1
FEB	15.0	0.7	35.1	8.8	22.1	28.6
MAR	19.2	1.9	42.6	13.8	21.1	15.9
APR	19.2	2.4	31.6	16.0	6.1	5.2
MAY	24.8	13.7	38.7	19.0	12.2	17.2
JUN	20.6	12.7	30.7	14.1	14.4	13.5
	r_S=0.4 n.s.		r_S=0.52 n.s.		r_S=0.86 p<0.005	

FIGURE 3.2.2

Mean ± 1.s.e. monthly total counts of choughs (colour- ringed or not) at Roost 1 from March 1985 to February 1988. Sample sizes can be found in Appendix 1.

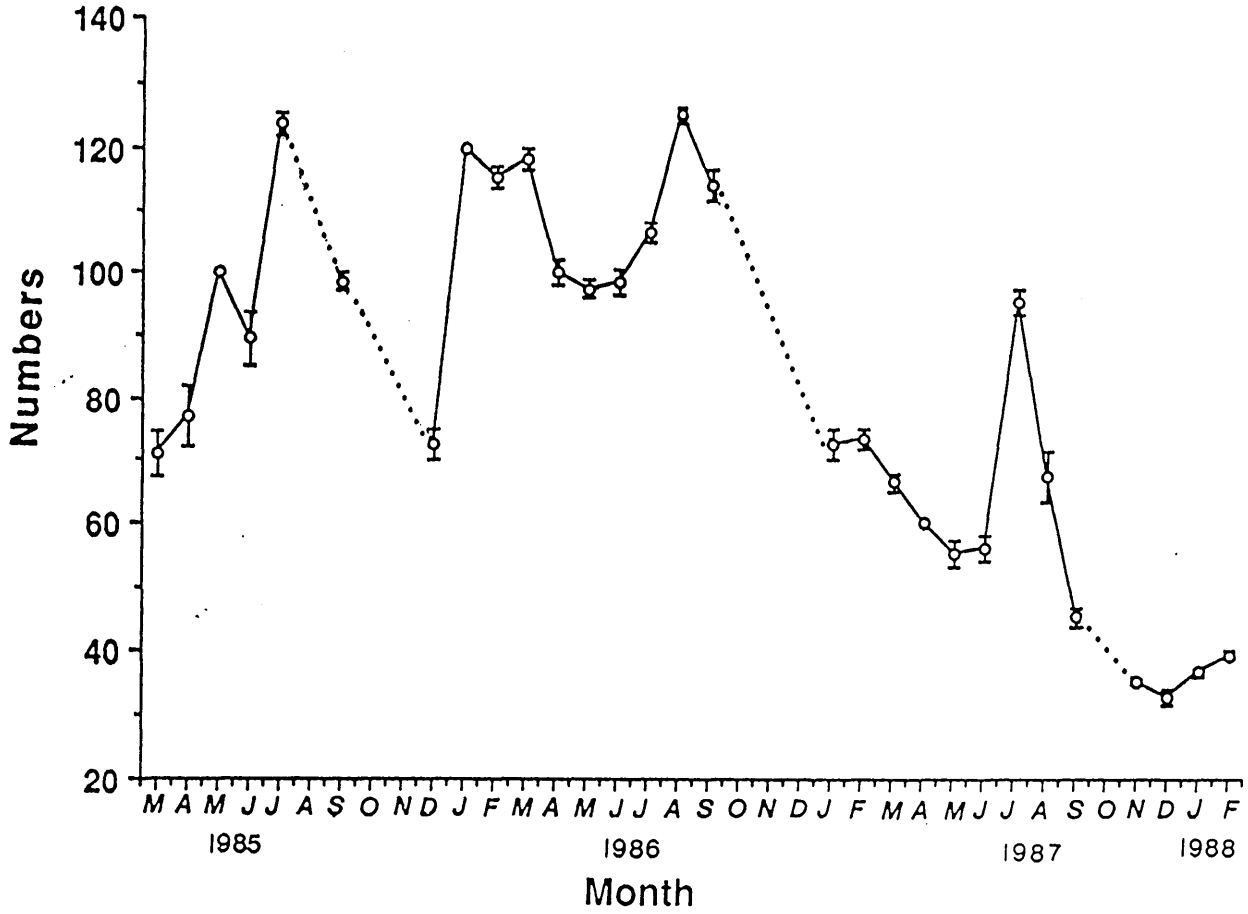

140
120
100
80
60
40
20
Numbers
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F
1985
1986
1987
1988
Month

FIGURE 3.2.3

The mean ± 1 s.e. monthly corrected numbers (see text Section 3.2.1 for details)) of first and second year choughs at Roost 1. Data for each of the two ages are a combination of different cohorts at the same respective age.

The data for the first June shows the numbers of the cohort in their previous year (as a choughs age increased in July). The second June shows the numbers of that cohort when they become a year older. For first year birds the first June shows that none were present at the roost as this was before fledged choughs were sighted at the roost. Full data (including sample sizes) can be found in Appendix 1.

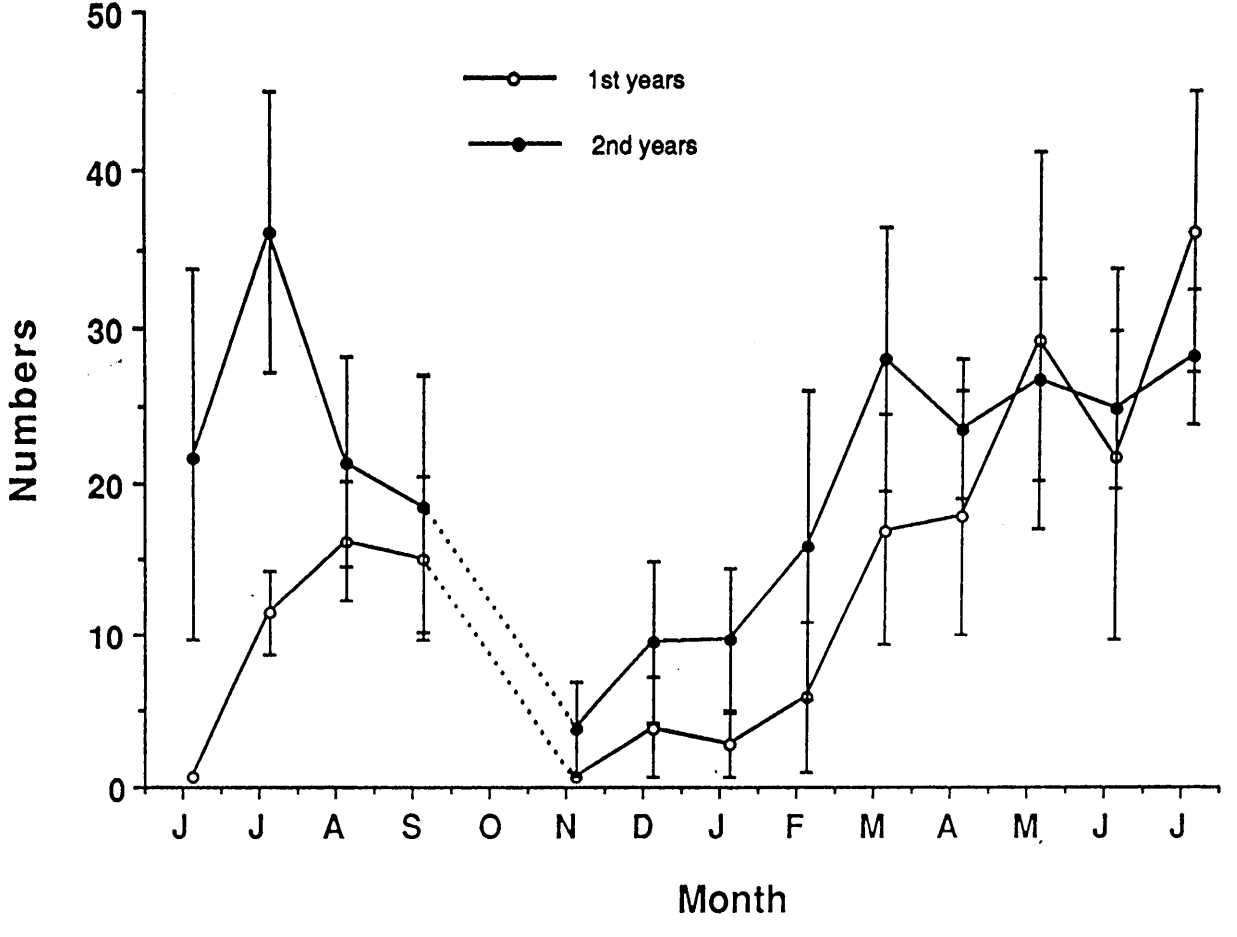

50
40
30
20
10
0
Numbers
1st years
2nd years
J
J
A
S
O
N
D
J
F
M
A
M
J
J
Month

FIGURE 3.2.4

The mean $\pm$ 1 s.e. monthly corrected numbers (see text Section 3.2.1 for details)) of third, fourth and fifth year choughs at Roost 1. Data for each of the three ages are a combination of different cohorts at the same respective age.

The data for the first June shows the numbers of the cohort in their previous year (as a choughs age increased in July). The second June shows the numbers of that cohort when they become a year older.
Full data (including sample sizes) can be found in Appendix 1.

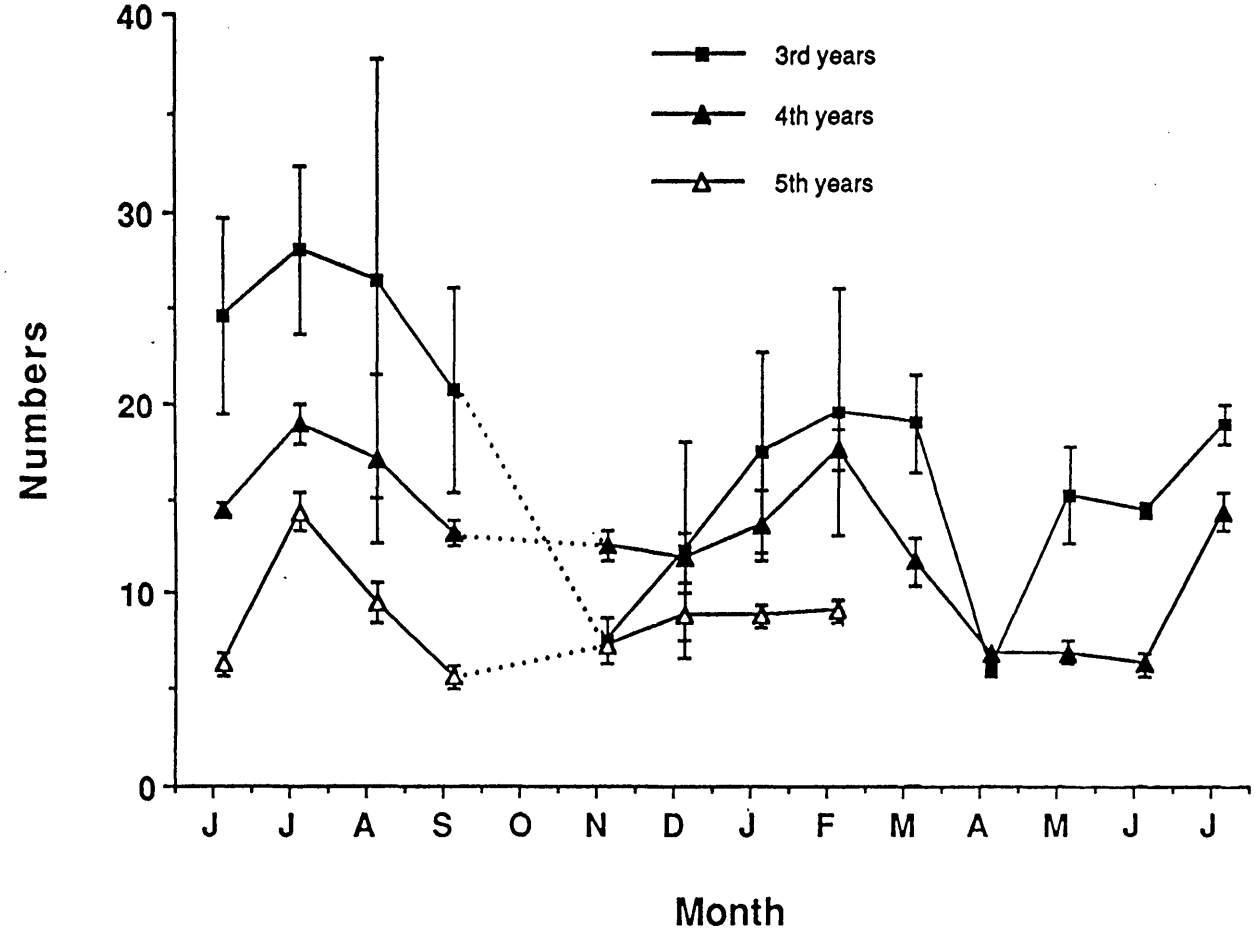

40
30
20
10
0
Numbers
3rd years
4th years
5th years
J
J
A
S
O
N
D
J
F
M
A
M
J
J
Month

FIGURE 3.2.5

Mean ± 1 s.e monthly corrected numbers (see text Section 3.2.1 for details) of first year choughs of different cohorts at Roost 1.

Full data (including sample sizes) can be found in Appendix 1.

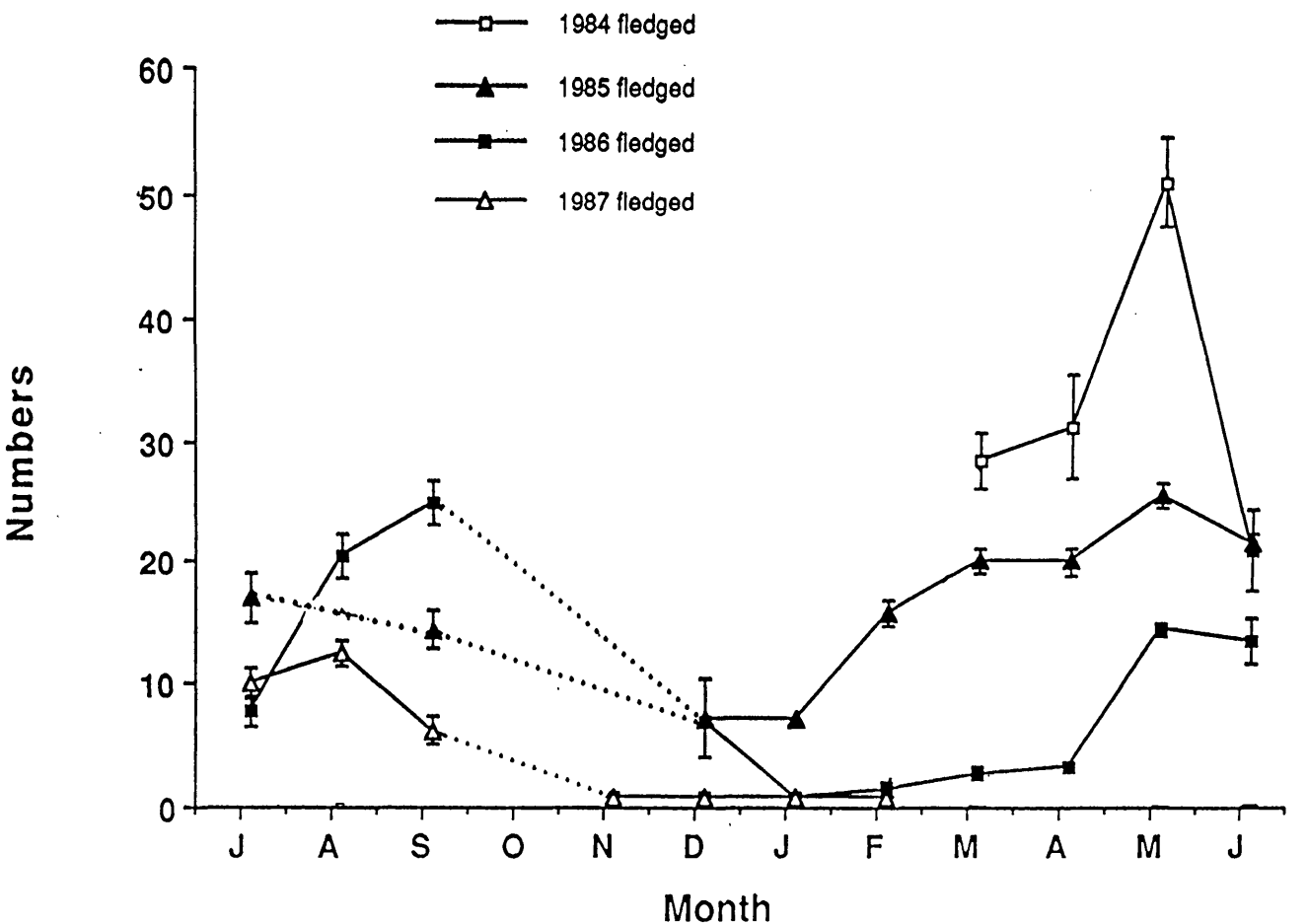

1984 fledged
1985 fledged
1986 fledged
1987 fledged
Numbers
60
50
40
30
20
10
0
J
A
S
O
N
D
J
F
M
A
M
J
Month

FIGURE 3.2.6

Mean ± 1 s.e monthly corrected numbers (see text Section 3.2.1 for details) of second year choughs of different cohorts at Roost 1. Full data (including sample sizes) can be found in Appendix 1.

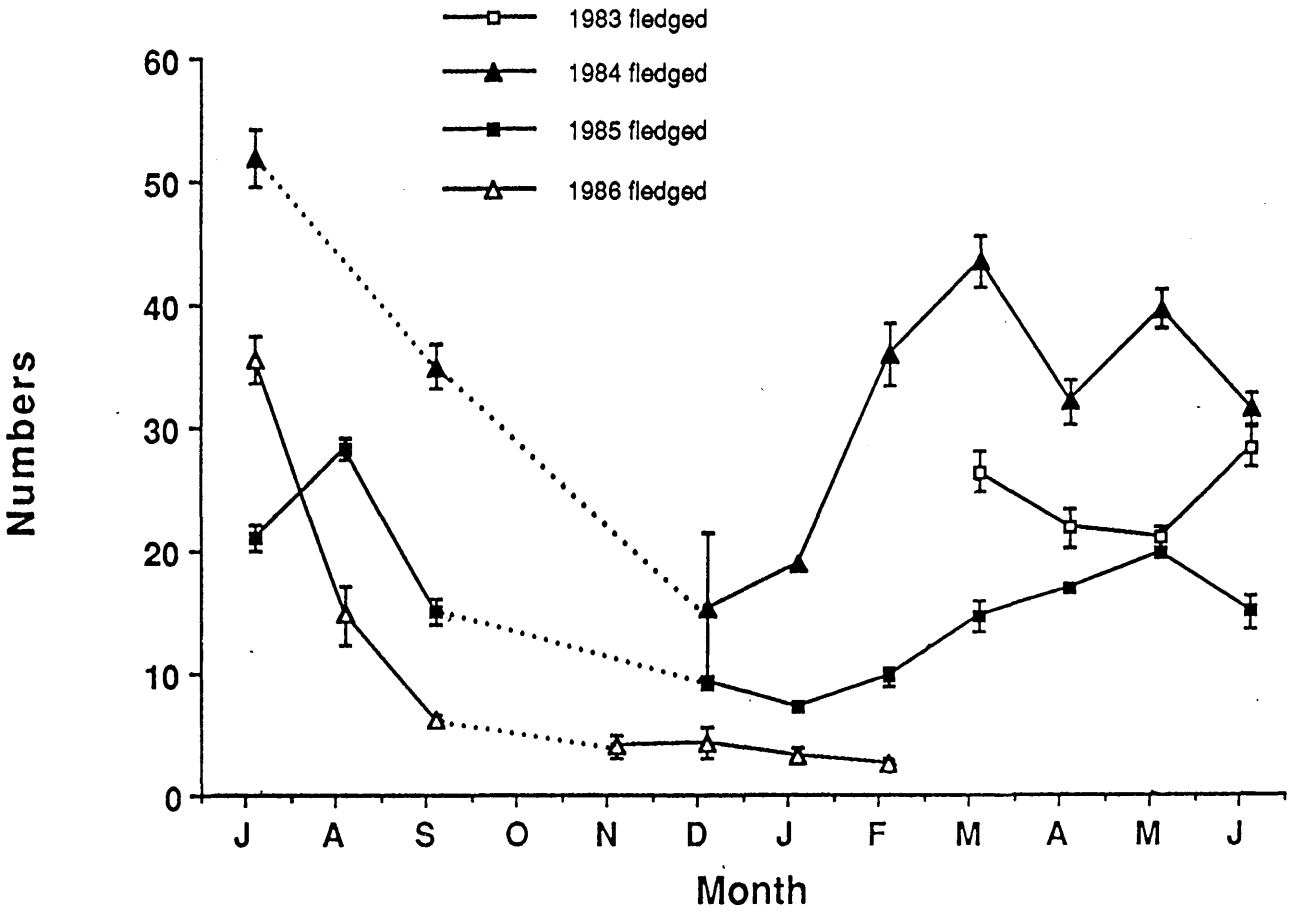

1983 fledged
1984 fledged
1985 fledged
1986 fledged
Numbers
60
50
40
30
20
10
0
J
A
S
O
N
D
J
F
M
A
M
J
Month

FIGURE 3.2.7

Mean ± 1 s.e monthly corrected numbers (see text Section 3.2.1 for details) of third year choughs of different cohorts at Roost 1.

Full data (including sample sizes) can be found in Appendix 1.

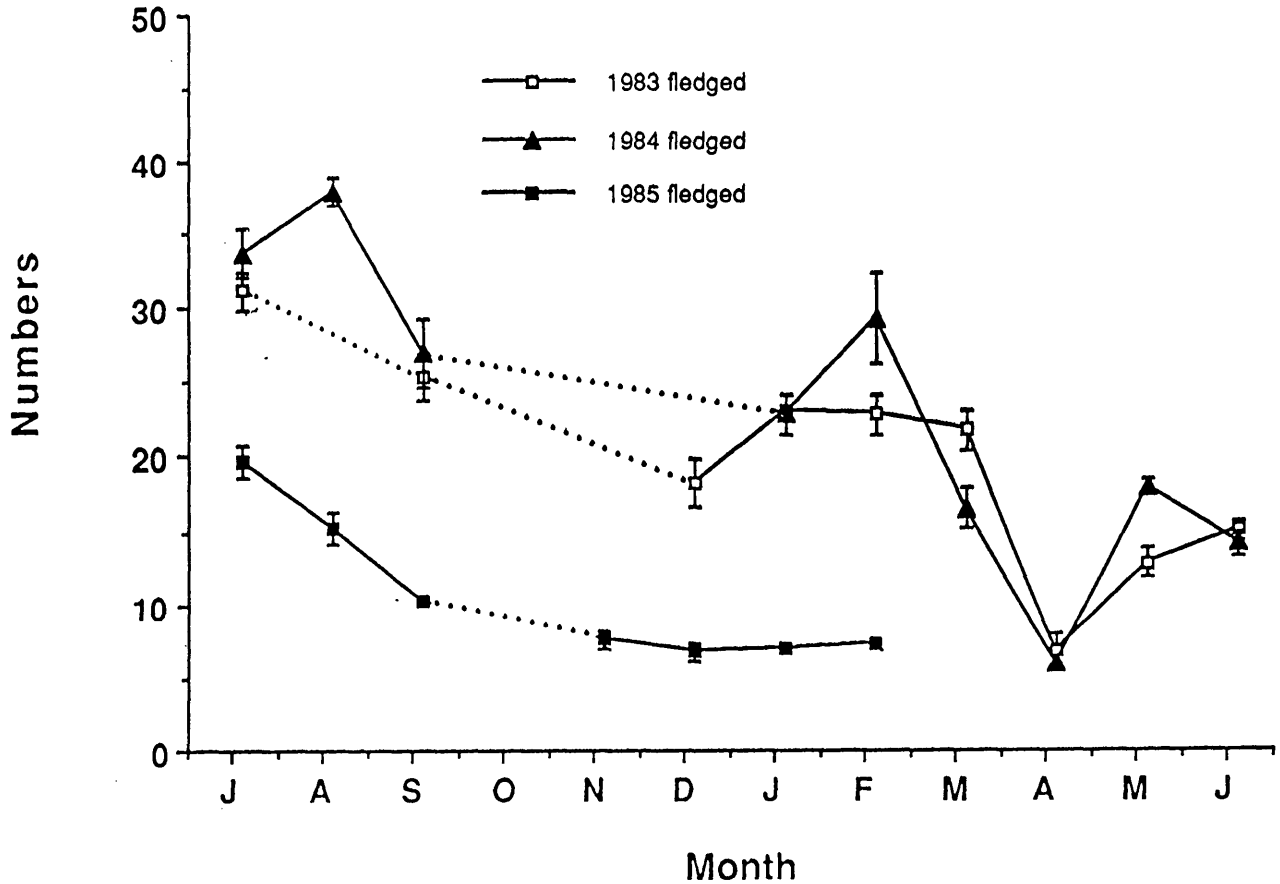
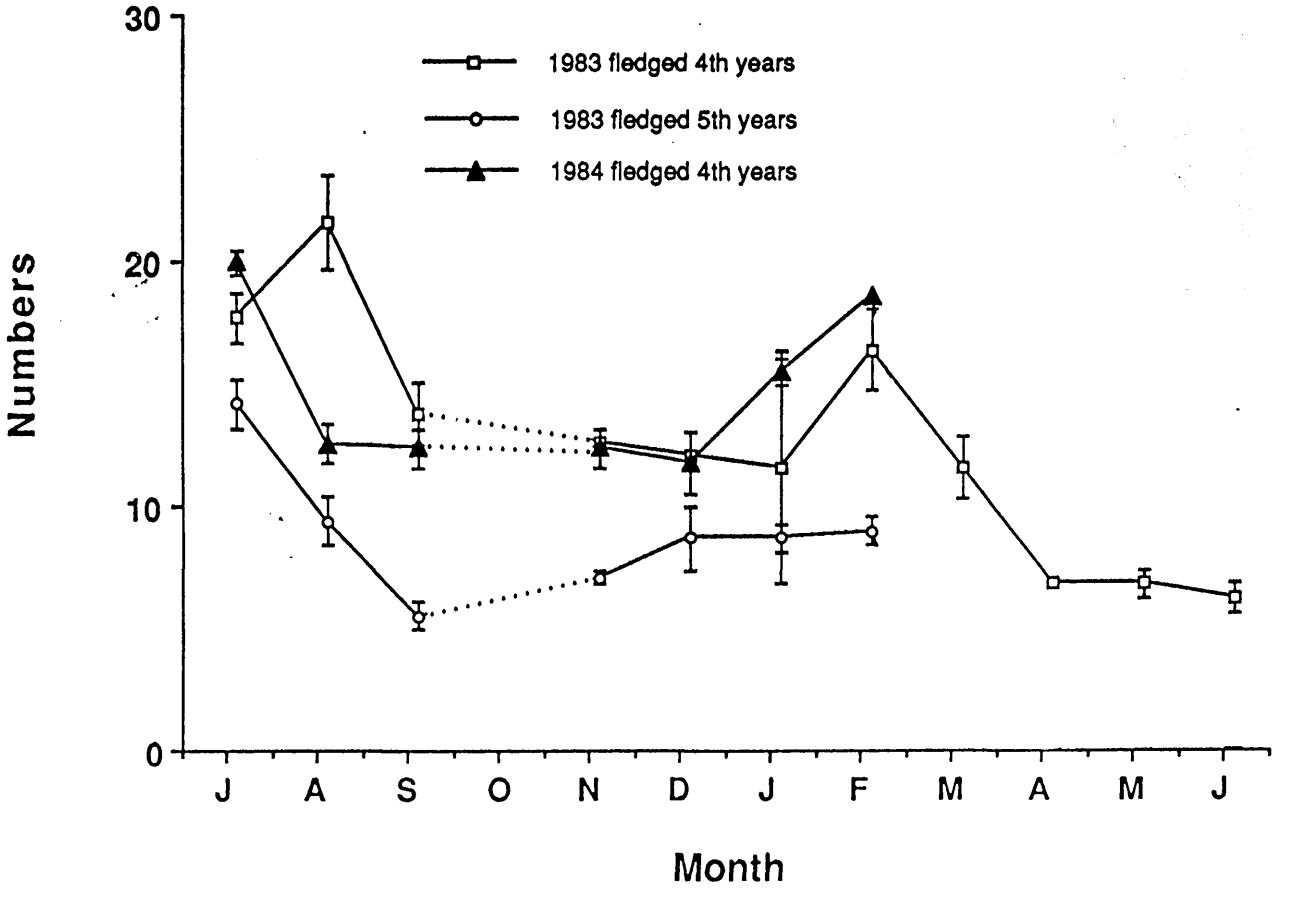

50
40
30
20
10
0
Numbers
1983 fledged
1984 fledged
1985 fledged
J
A
S
O
N
D
J
F
M
A
M
J
Month

FIGURE 3.2.8

Mean $\pm$ 1 s.e monthly corrected numbers (see text Section 3.2.1 for details) of fourth and fifth year choughs of different cohorts at Roost 1. Data for fifth year choughs are for one cohort only.

Full data (including sample sizes) can be found in Appendix 1.


30
20
10
0
Numbers
1983 fledged 4th years
1983 fledged 5th years
1984 fledged 4th years
J
A
S
O
N
D
J
F
M
A
M
J
Month

3.2.2 DISCUSSION.

The reason for the overall trend for a decrease in the roosting numbers is not known. There is no evidence to suggest that there is a decrease in actual numbers of birds on the island. In fact the population seems to be on the increase, (Warnes 1983a,b, Bignal *et al.* 1987, Monaghan *et al.* 1989) especially in the proportion of non-breeders in the population. There has been an increase in the numbers of birds using other roosts especially young birds immediately after fledging and over the winter/spring period (pers. obs.). This fragmentation of the largest roost into smaller roosts may be due to changes in food availability especially over the winter period as, although numbers dropped at the study roost over the winter period, the most recent counts suggest that they are still returning to levels approximating the summer roost flock size which was seen in 1985 and 1986 (Figure 3.2.2). However, the largest decrease in roost size was over the 1986/1987 winter months and since then the numbers have never regained their former strength.

It cannot be ignored that differences in fledging success may have affected the accuracy of the estimated proportions of ringed choughs in a given cohort since fledging success was assumed to be constant between years. This in turn will affect the corrected numbers of each cohort calculated from the numbers of ringed choughs. It is certain however that these differences do not account for the sometimes large variations between years. Differences in the age composition of the roosting flock, (Figures 3.2.5 to 3.2.8), in different years suggest that there are changing influences on the choughs from year to year. These influences may thus affect their behaviour.

Movements of choughs to other areas may vary from year to year possibly affected by the availability of food, competition for food around this roost or competition for roost sites within the roost. The availability of food or presence of

competition for food may affect birds differentially depending on their age. For example the 1986 fledged choughs moved away from the roost during their first winter almost entirely, only returning to the roost the following summer at a time when the 1987 cohort were also arriving at the roost. During the winter of their second year, the 1986 cohort moved away again to another area. This suggests that, for at least the 1986 cohort, choughs seem to be acting together as a cohort, as the majority of the 1986 cohort still roosted and fed together in another part of the island. This pattern of movement by a cohort is also true for the 1987 cohort, as numbers fell at the roost from August of their first year from a maximum of 22.8% of the population to 0% during the winter between November and the following February.

First and second year birds show a remarkably similar pattern in their use of the roost within a year, with numbers decreasing over winter and increasing again in late spring/summer. The majority of choughs do not usually start to breed until their third year (Bullock *et al.* 1983a) although a few second years do attempt breeding but are usually unsuccessful. Therefore the majority of second years and all first years are of pre- breeding age and may behave in a similar way.

Third, fourth and fifth year birds also show a similar pattern of roost use to each other although numbers of third years fluctuate more relative to the older birds. However, the pattern of roost use by a given age class can vary between years, at least for first and second year choughs. This may relate to changing feeding opportunities. The movement of birds is examined in more detail in the following sections.

In summary:-

There was an overall trend for a decrease in the numbers if choughs using the roost over the study period. Peaks in numbers occurred between June and August.

Numbers of 1st and 2nd year choughs were at a minimum over the winter period with the lowest numbers present between November and January.

Numbers of 3rd years also dropped during the winter although less markedly than for younger choughs.

The numbers of 4th and 5th year choughs showed relatively little decline during the winter compared to younger choughs.

3.3 MOVEMENTS OF BIRDS TO AND FROM THE COMMUNAL ROOST.

3.3.1 INTRODUCTION.

The fluctuations in numbers of choughs attending the roost as observed above are likely to be due to birds moving to new foraging areas or occupying breeding sites. Some of the decline in numbers, particularly in the post-fledging period, is likely to be due to mortality. The reasons for the observed variation in numbers using the roost was investigated by examining the behaviour of individual birds in detail.

3.3.2 METHODS.

The arrivals and departures of individual colour- ringed choughs at Roost 1 were examined on a monthly basis. Only months with three or more observation nights at the roost were included in the analysis. If a bird was seen during that month it was classed as present at the roost during that month. If, however there were no further sightings of a bird at the roost in a month within which at least two more roost

visits were made in that month after the last sighting, and the bird was not present the following month, it was classed as having left the roost during the former month.

Based on additional sightings of the birds away from the roost (particularly during surveys- see section 4.2), choughs leaving the roost could be classed as:

a) Leaving to breed (successful or unsuccessful nesting attempt)
b) Leaving to hold or visit a potential nest site/territory (no breeding attempt)
c) Leaving to join another flock roosting at another site
d) Leaving for unknown reason (ie. location unknown) but still alive i.e. found later but not known whether they held territory or joined non-breeding flock
e) Leaving and not seen subsequently.

Choughs arriving at the roost were classed as:
a) Arriving from a breeding attempt, either with or without young
b) Arriving from holding or visiting a potential nest site/territory
c) Arriving from another flock roosting at another site
d) Arriving from an unknown location.

Data collected from February 1986 - February 1988 were used in the analyses.

3.3.3 RESULTS.

The highest percentage of departures from the roost in this more detailed examination occurred in the autumn/winter from September to January (Figure 3.3.1b) At this time few choughs arrived (Figure 3.3.1a). Overall the highest numbers of departures by young choughs (1st - 3rd yrs.) which were seen again tended to be to other flocks (Appendix 2). For older birds, departures tended to be to territories and breeding sites. Older birds which were not seen again may have moved to territories. These were not seen again possibly because of poorer coverage

FIGURE 3.3.1a

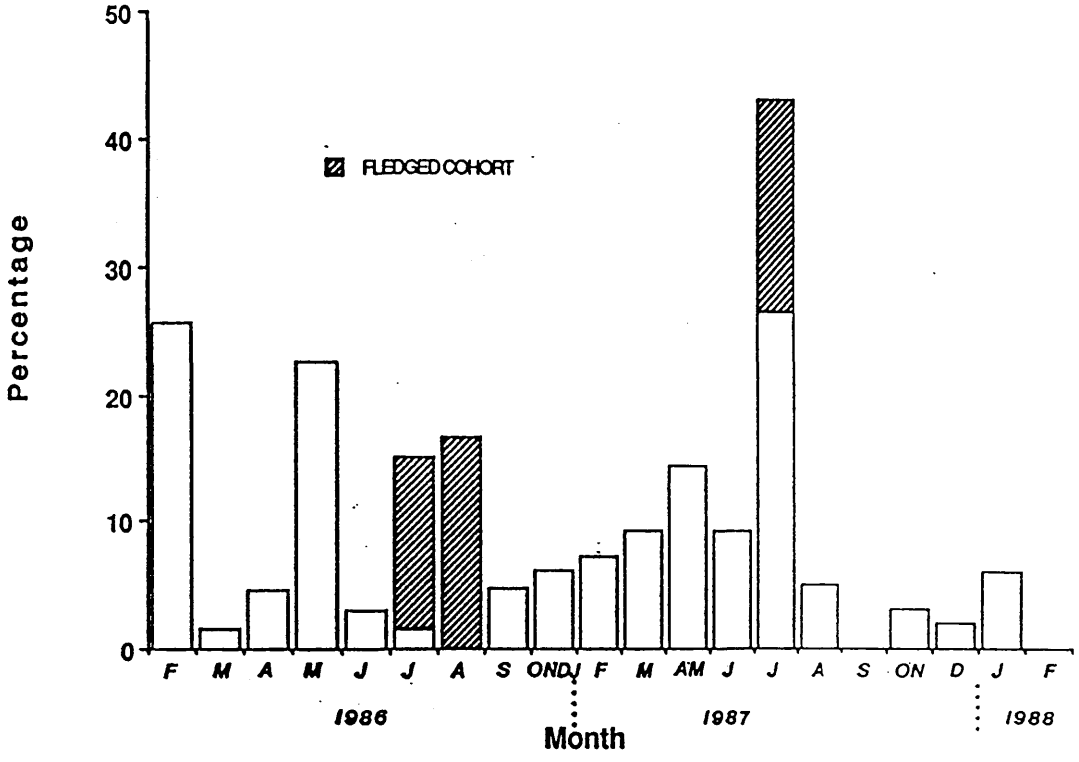
The monthly percentage of arrivals to Roost 1. The monthly data show the percentage of arrivals over each year which occurred in that month. Data for January and February 1988 are percentages of the 1987 years arrivals. Sample size = 110 bird arrivals.

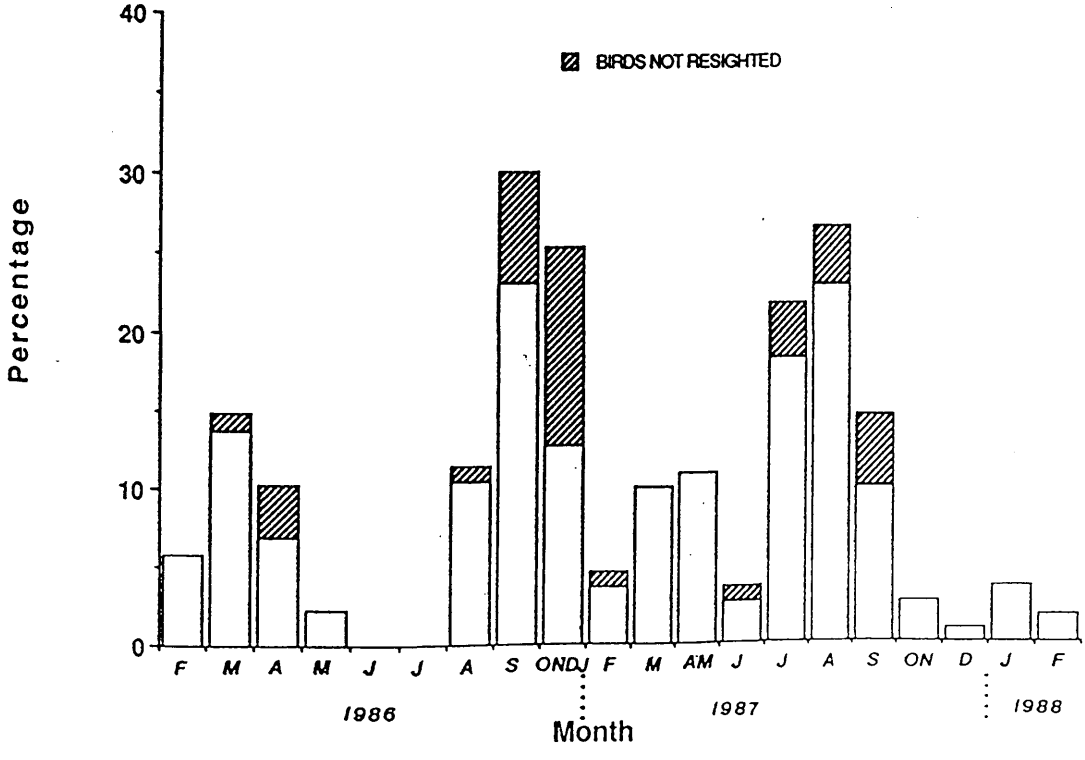
The percentage of arrivals which were newly fledged choughs are shown by shading. A breakdown of the origins of arriving choughs can be found in Appendix 2 for each age class.

FIGURE 3.3.1b

The monthly percentage of departures from Roost 1. The monthly data show the percentage of departures over each year which occurred in that month. Data for January and February 1988 are percentages of the 1987 years departures. Sample size = 87 bird departures.

The percentage of departures of choughs which were not resighted anywhere else are shown by shading. A breakdown of the locations of departed choughs can be found in Appendix 2 for each age class.


50
40
30
20
10
0
Percentage
FLEDGED COHORT
F M A M J J A S ONDJ F M AM J J A S ON D J F
1986
1987
1988
Month


40
30
20
10
0
Percentage
BIRDS NOT RESIGHTED
F M A M J J A S ONDJ F M AM J J A S ON D J F
1986
1987
1988
Month

of breeding sites outwith the breeding season relative to coverage of potential feeding areas of non-breeding birds. Of the departing birds not seen again between October 1986 and January 1987, all of them (11 birds) were first (8) and second year birds (3). Of the departures of birds not seen again from the roost in the three months after fledging 17/20 (85%) were newly fledged birds. .oj off

3.3.4 DISCUSSION.

Of the arrivals to the roost in July and August the highest proportion was made up of newly fledged birds. There was also a rise in numbers arriving to the roost during the late spring. Much of this rise is accounted for by young choughs arriving from other areas (see Appendix 2).

First year birds have a lower survival rate in their first four months (83%) than later in their first year (86%) and also lower than older birds (Bignal *et al.* 1987). Some of these departures by first year birds may well be due to mortality. First and second year birds in particular seem to show the greatest turnover at the roost. There seemed to be a large increase in the number of first year birds arriving at the roost from other areas in late spring/summer (Figures 3.2.3 and 3.3.1a).

Fourth and fifth year birds show less of a decrease in numbers over winter. As there are still birds in their fourth and fifth year which have not yet bred, the fact that there is less fluctuation suggests that these older choughs which remain in the area and use the roost form a regular core of older birds (also pers. obs.). The majority of movements by fourth and fifth year birds were birds returning to and from territories (which were held but no breeding attempt was made), leaving to breed or returning from failed breeding attempts. (Appendix 2). There was little movement of these older choughs to other feeding areas and roosts. Any movements by these birds were usually associated with prospecting away from the roost and joining other flocks to feed and roost in the process.

3.4. THE ROLE OF PREVIOUS EXPERIENCE IN THE USE OF A ROOST SITE.

3.4.1 INTRODUCTION.

As stated above there was an increase in the number of choughs arriving at the roost from other areas just before and during the period when the fledged choughs from the current breeding season were arriving at the roost. This was particularly marked among choughs which fledged the previous year (i.e. just into their second year).

These birds did not arrive at the roost with offspring of their own, and so must be arriving for another reason. One possibility is that there may be some form of "tradition" that birds return to the roost to which they came on fledging the previous year, and that they return again at fledging time the following year.

3.4.2 METHODS.

To investigate this, choughs which fledged in 1985 and 1986 were classed in four categories:

a) Birds which fledged and arrived at Roost 1 during the first three months after fledging;

   i. then returned the following fledging period.

   ii. then did not return the following fledging period.

b) Birds which did not arrive at Roost 1 during the first three months after fledging;

   i. then arrived at Roost 1 the following fledging period.

   ii. did not arrive at Roost 1 the following fledging period.

3.4.3 RESULTS.

The numbers of ringed choughs which fledged each year were known. However, of those which fledged there is only 83% survival within the first three months after fledging and of these which survive the first three months, 86% survival during the remaining nine months. (Bignal *et al.* 1987). This allows the calculation of the numbers *expected* to still be alive even though they were not sighted at the roost during their first year.

Tables 3.4.1a & b. The numbers of 1985 and 1986 fledged second year colour-ringed choughs returning to the communal roost at Roost 1. Numbers *expected* are calculated from survival rates.

3.4.1a. 1985 fledged birds.

Numbers fledging July = 85
Numbers *expected* to survive July - September (83%) = 70

Numbers arriving at Roost 1 (July - September)	Numbers going elsewhere (July - September)
37	33
Numbers *expected* to survive the remaining 9 months (86%)	Numbers *expected* to survive the remaining 9 months (86%)
32	28

Returning 1986	Not returning 1986	Arriving 1986	Not arriving 1986
15	17	11	17

$X^2 = 0.34$ (1 d.f.) n.s.

3.4.1b 1986 fledged birds.

Numbers fledging July = 61
Numbers *expected* to survive July - September (83%) = 51

Numbers arriving at Roost 1 (July - September)	Numbers going elsewhere (July - September)
24	27
Numbers *expected* to survive the remaining 9 months (86%)	Numbers *expected* to survive the remaining 9 months (86%)
21	22

Returning 1986	Not returning 1986	Arriving 1986	Not arriving 1986
7	14	15	7

$X^2 = 5.1$ (1 d.f.) $p < 0.02$

The results shown in Table 3.4.1a relate to birds which fledged in 1985 and in Table 3.4.1b to birds which fledged in 1986. These data show that choughs which fledge to Roost 1 were not significantly more likely to return the following fledging period than birds which did not arrive there after fledging. Table 3.4.1b however suggests that, in fact, choughs which did not fledge to Roost 1 may have been *more* likely to return to Roost 1 the following year than birds which did fledge to Roost 1.

3.4.4 DISCUSSION.

The above result is difficult to interpret and should be treated with caution. However, there are a number of ways in which these results could be interpreted. Young birds which had never been to Roost 1 did in fact arrive together with birds which had been previously to Roost 1. There are two possible explanations for this. One is that although birds were returning in large numbers from other areas, individuals may have been making independent choices as to where they move to and may have arrived in feeding areas around Roost 1 purely by chance and, if food availability is high, may decide to stay. Another possibility is that birds which had not been to Roost 1 ("naive birds") arrived with others which have previously been to Roost 1. These "naive" birds were known to roost (at Roost 2) and feed with birds which had fledged to Roost 1 the previous year. The naive birds may have followed these others to Roost 1 and the surrounding feeding area. Acting as a cohesive flock, the naive birds followed others which may have been knowledgeable about potential food availability in other areas. This may provide a useful function to naive birds in the location of new food sources and be an advantage to them in flocking (Sabine 1956).

If roosts are in traditional locations as has been observed with many species such

as starlings, some geese (*Anser* spp. and *Branta* spp.) and rooks *Corvus frugilegus*, it may be easier for birds, especially those which split into sub-groups to feed, to locate a traditional roost site. Advantages to improved foraging success, especially if food availability is high over a relatively long period around the roost may result from birds being able to easily find a roost which is in a constant location rather than a constantly changing roost location. The fact that roost locations are often in traditional sites indicates that either food availability in the surrounding area is high or that there is a lack of other suitable roost sites. in traditional sites suggests

3.5. ROOST DYNAMICS - GENERAL DISCUSSION.

At this point it may be worth summing up the results of the previous sections. The decrease in numbers of choughs using the roost during the winter months may be due to choughs moving to other areas during this period. This suggests that the food supply surrounding this roost may not be as plentiful or as suitable as in other areas. As the largest decrease in numbers over winter is produced by first and second year birds leaving the roost it may be that, possibly due to competition for limited food resources, these birds may be forced out of the area. High proportions of young birds are found at other roosts. Competition from older birds may cause subordinate, younger birds to forage in secondary areas (Lockie 1956, Davis 1975, Monaghan 1980, Baker *et al.* 1981, Ewald 1985, Eden 1987). The fact that there is less decrease in the numbers of third, but particularly fourth and fifth year birds from the roost (and birds which do leave tend to go to territories rather than other feeding flocks) suggests that there is no advantage in older birds leaving the area. A knowledge of feeding sites surrounding the roost may be an advantage to these older birds and may mean that for them, less time has to be spent looking for good feeding sites. The movement of subordinate birds to and from flocks has been

noted in several species e.g. black-capped chickadees *Parus atricapillus* (Smith 1984).

The increase in the numbers of birds arriving to the roost during the fledging period may be due to an increase in the availability of food in the area surrounding the roost. This may also explain why breeding birds return to this roost with their fledged young. During the fledging period the area surrounding Roost 1 has a large number of fields which are being cut for silage. The cutting of the silage allows access to food sources, particularly soil invertebrates, which were unavailable during the previous months due to the grass length being in excess of the maximum height in which choughs prefer to feed (Bullock 1980). The return of older birds to the roost (in particular the second year birds) may also in part be due to the local enhancement of the area by breeders and newly fledged birds arriving in the area. The decrease in the number of 3rd and 4th year choughs in the spring may be due to these older choughs moving out of the non-breeding flock in search of a territory. The fact that a proportion of third years return may suggest that they are not all successful in finding or defending a territory. The increase in numbers of 4th years as they become 5th years in July may be accounted for by breeders returning to the communal roost with their offspring. Of the maximum number of nine colour-ringed 5th years seen at the communal roost in July 1987 four had returned with young and one returned briefly after a failed breeding attempt.

The above results show that a roosting flock of choughs is not a static system but numbers of birds and age composition of the flock changes throughout the year. These changes are influenced by changes in behaviour of birds as they get older (i.e. moving away to hold a territory, to breed or to join another flock and returning after a failed or successful breeding attempt, or from another flock. Food availability and competition for food which are dependent on season and farming practices, also presumably play a part in the roost flock dynamics.

3.6 SOCIAL STRUCTURE AT THE ROOST

3.6.1 INTRODUCTION.

In avian species which roost communally, differences in the dominance of individual birds may manifest themselves in observable agonistic interactions. Such competition within the roosting flock may be the result of differences in the quality of these roosting positions. Quality differences may be in microclimate (Yom-Tov *et al.* 1977, Gyllin *et al.* 1977, Swingland 1977, Walsberg 1986) or in the superiority of roost sites in predator avoidance (Crook 1965, Lack 1968, Hamilton 1971, Bertram 1978, Weatherhead 1983). Wynne-Edwards (1962) found that individual starlings maintained the same roost site for a succession of nights.

Roost sites may also carry some form of social distinction which is as yet unknown as birds often maintain the same roost site from night to night and in some cases over a number of months (Warnes 1983a, this study).

Differences in the spatial positions of birds of different sex, age and physical condition within communal roosts have been noted in several species; choughs (Still *et al.* 1987), waders (Furness & Galbraith 1980, Swennen 1984), rooks (Swingland 1977), red- winged blackbirds, *Agelaius phoeniceus* (Weatherhead & Hoysak 1984) and starlings (Summers *et al.* 1987). Older birds, males and birds in better body condition tend to be found in the centre or densest parts of communal roosts and this dispersion pattern has been attributed to the relatively higher dominance of these birds. These authors suggest that these central birds gain a greater predator avoidance level by roosting in such places.

Observation of aggressive interactions between individuals within a roosting flock can give an indication as to dominance hierarchies and level of competition

for roost sites, and thus some indication of the relative benefits and disadvantages accorded to individuals roosting communally.

From earlier work (Still *et al.* 1987) over a short period it was found that choughs tended to roost with birds of the same age. Older birds roosted in the densest area of the roost flock although the division between age classes was a more obvious feature than central roosting by older birds and peripheral roosting by younger birds. From continuing observations at the largest, regular roost (Roost 1) over a longer period, it became clear that there was more movement by age classes within the roost although birds of the same age class tended to stay together. This aspect of the choughs roosting behaviour was examined in detail.

3.6.2 METHODS.

All observations of aggressive interactions were carried out at Roost 1. This was the only roost where clear visibility of the roost cliff allowed birds to be observed for any length of time before and after they had settled on the cliff. A full description of the cliff and observation methods can be found in the Section 2.3.

A total of 2037 one minute observation sampling periods were carried out on individually colour-ringed birds between 18/4/86 and 8/2/88 with no more than two one minute sample periods per bird per observation night. Only focal periods during which the bird was in full view for the entire minute were used in the analyses. The identity of each focal bird was recorded as well as information as to whether it was settled in a roost site or not. Settled birds were classed as those which were in a known roost site (used by that, or any other bird previously and often recognised by droppings under the site). Settled birds also included those

observed to be asleep (head resting on back, one foot raised under the body, or the bird hunched up with or without its eyes closed). Birds were classed as not being settled if they were moving around or above the roost cliff, or perched alert and not in a known roosting area. If a bird changed from being settled or not settled during the focal observation its status at the start of the interaction was recorded. If, however, no interaction occurred then the status of the bird at the start of the focal period was the one recorded.

If an aggressive interaction occurred, the identity of the bird which initiated the interaction was recorded as was the recipient where possible although interactions were often over quickly. An bird which initiated was classed as the bird which made the first threat to the other participant thus causing an aggressive interaction. This could be a movement toward the other bird, a lunge, a kick with a foot or a peck. Threats were also classed as aggressive interaction. However, if the result of the interaction was not clear, (such as the participating birds moving away from the roost or out of view), the interaction was not used in the analyses.

The bird which won an aggressive interaction was taken as the bird which maintained its roost site or took over a roost site from the other bird. If a bird chased the other bird away from the cliff and then returned to the cliff either settling in the same roost site, a different one or not settling, it was also classed as the winner. The only problem here is recognising the winner if it did not return to a roost site as classified above. In these cases the winner is taken to be the bird doing the chasing. If any doubt occurred, the interaction was discarded. For an interaction to escalate to a chase it seems reasonable to assume that the bird doing the chasing is the dominant bird. If an aggressive interaction occurred during a focal period, the birds were observed until the interaction was over even though this may have been over the one minute sample period. As the interaction started during the minute observation period and data analyses was not related to time spent in

interactions but rather to frequency and outcome, it was necessary to continue any observation of an interaction over the one minute sample period to obtain data on the outcome. The observation was then stopped after the outcome was decided. A new focal observation was then started. Aggressive interactions were classed as passive supplantations or avoidances, threats (lunges, attempted pecks or kicks), or physical contact between the participants.

The data were split into three periods: 18/4/86 to 30/6/86, 1/7/86 to 30/6/87, and 4/7/87 to 8/2/88. These periods were used to enable classification of birds by their age, as the earliest date of arrival of newly fledged birds to the roost was within the first few days of July. This is explained in more detail in Section 2.4. Thus, after the 1st July birds were classed as a year older and the newly fledged birds classed as first years.

The following parameters were calculated:

Dominance index - The number of aggressive interactions an individual won (as the focal bird) divided by the total number of aggressive interactions it was involved in (when it was the focal bird). The minimum total number of aggressive interactions used to calculate the mean dominance index for each bird was five. The larger the dominance index value, the more "dominant" the individual.

Arrival score - As the birds arrived at the roost the identity of each marked bird was recorded. This gave a relative order of arrival to the roost. Although not an accurate measure as birds often arrived in large groups and the precise order could not be determined, over many observation nights at the roost a pattern could be discerned. The ordered number of marked birds each night was split into thirds with the final third containing the remainder if the list was not divisible by three. This last third contained either one more or one less than either of the first two

thirds and this inaccuracy was evened out over the period. Birds arriving in the first third were given a score of 1, the second third a score of 2 and the final third a score of 3. A mean relative arrival score could therefore be determined for each individual bird. The arrival score could thus range from a minimum of one to a maximum of three. The lower the score or mean score, the earlier a bird was observed at the roost. The minimum number of arrival scores used to calculate the mean for each bird was ten.

Site fidelity - The positions of colour ringed birds were recorded each night after they were resident in a roost site. This was done just before leaving the roost after an observation night and before the light conditions were too poor to accurately identify birds. At this time, movement of birds around the roost and changing of roost sites did not occur to any extent although it cannot be totally ruled out. Site fidelity was calculated as follows; the number of different roost positions recorded for each bird was divided by the total number of times a roost site position was plotted for each bird. For example, one bird may have used four different roost sites over a period when on twenty nights a roosting position was recorded. This bird then receives a site fidelity score of 4/20 = 0.20. (Despite the fact that this index does not take into account the usage of these four sites by the bird who may have used one site seventeen times and the other three sites only once each, it gives a useful index of site fidelity.). The smaller the site fidelity index, the more site faithful the bird, the maximum index being one. The minimum number of observations used to calculate a mean site fidelity index was ten.

Associations between age classes. The following analysis was carried out to examine age-related relationships between roosting choughs. Ideally, nearest neighbour analysis would have been carried out to examine these relationships, however this could not be done due to the reasons set out below.

When studying nearest neighbour distances (or in this case second nearest

neighbour) using actual distance measurements, an important factor which is needed for this calculation is the density of individuals within the sample unit. Another important consideration is the edge effect caused by taking a sample unit from within a larger population (Ripley 1981, Upton & Fingleton 1985). As density within the sample unit probably changed from night to night and the results were combined over a number of nights, actual distance measurements could not be used in any analyses. There was no need to consider edge effect as the sample unit was the whole population (roost flock). Because densities could not be calculated for each observation night at the roost, an alternative method had to be used to examine associations between roosting choughs.

The distances between each marked bird and its second nearest colour-ringed neighbour each night were calculated. Second nearest neighbour distances were used to prevent paired birds which were both marked and habitually roosting close to each other biasing the data. For example, a second year bird constantly roosting with a fourth year mate and being its nearest neighbour would bias the data in the overall spatial relationship between second and fourth year birds. Paired marked birds in fact did not always roost together, although close roosting was regularly observed for a number of pairs.

The null hypothesis was that birds did not preferentially roost with birds of the same age. For this to be examined, it was necessary to calculate the probability of a bird roosting with another bird of the same age purely by chance. The formula used to calculate this is set out below:

$$\frac{A_n - 1}{F - 1} \times A_n$$

where:-
A_n = number of colour ringed birds in a chosen age class on a given night.
F = total number of colour ringed birds (of all age classes combined) on a given night.

From this it is possible to calculate expected numbers of birds of each age class which, purely by chance, should be the second nearest colour-ringed neighbour of any particular bird. Each night the second nearest colour-ringed neighbour of each bird was identified. For each age class on each night the data were combined to provide the total number second nearest colour-ringed neighbours which were the same age or different age. From there, this total was then combined over a numbe of nights to provide a seasonal total. A Sign Test was then carried out to establish whether the numbers of second nearest neighbours which were the same age or different age were greater or less than the calculated expected.

3.6.3 RESULTS.

The results of aggressive interactions are shown in Table 3.6.1. The data are split into four age classes. There were no significant differences in the behaviour of cohorts at the same age therefore the data were combined across cohorts. First, 2nd and 3rd year age class data are combination of data from three cohorts at the same age; the 4th/5th year data are a combination of data from two cohorts at age 4 and one cohort at age 5.

There was a significant difference in the numbers of aggressive interactions won and lost by the four age classes with older birds winning more and losing fewer aggressive interactions than younger birds (Table 3.6.1).

Using a null hypothesis that there should be an equal chance of winning and losing, the proportion of encounters won can be examined for each age class using a goodness of fit test with 50:50 being the expected ratio. Tables 3.6.2a-d display the appropriate numbers of wins and losses in aggressive interactions for each age

class. Fourth and fifth year birds won significantly more aggressive interactions than they lost, as did 3rd years, (Tables 3.6.2a & b respectively). Second and first year birds lost significantly more aggressive interactions than they won, (Tables 3.6.2c & d respectively).

Table 3.6.3 shows the numbers of aggressive interactions initiated or not initiated by the four age classes of choughs. There was a significant difference in the numbers of aggressive interactions initiated by the four age classes with older birds initiating a larger proportion of the aggressive interactions they were involved in than younger birds.

Table 3.6.4 shows the numbers of aggressive interactions initiated by the four age classes which were won or lost by the bird initiating the interaction. There was a significant difference between age classes with older birds winning more aggressive interactions which they initiated than younger birds. Older choughs also won a larger proportion of their aggressive interactions if they were settled in a roost site than younger birds (Table 3.6.5). In fact 1st and 2nd year birds lost more aggressive interactions than they won when settled in a roost site.

Table 3.6.6 shows the numbers of interactions which involved the three categories of aggressive interaction identified. There were significantly more passive supplantations / avoidances, more threats and fewer physical contacts than an expected equal ratio although deciding what is an expected value in an analyses such as this is purely arbitrary.

Figure 3.6.1 shows the relationship between age and dominance index. The mean dominance index for each age class was calculated from the mean dominance index of all birds of that age class. As would be expected from the previous results, there

was a significant trend for older birds to have a higher dominance index than younger birds (r_S = 0.65, $p < 0.001$ 55 d.f.).

Figure 3.6.2 shows the relationship between age and arrival score. The mean arrival score for each age class was obtained at by calculating the overall mean derived from the mean arrival scores for each individual of that age class. There was a significant trend for older birds to arrive later than younger birds although the trend levels out after age 2 (r_S = 0.73 $p < 0.001$ 125 d.f.).

Figure 3.6.3 shows the mean site fidelity index plotted against age class. Older birds had a lower site fidelity index than younger birds (r_S = 0.52 $p < 0.001$ 115 d.f.). (The smaller the index the more site faithful the bird).

Relationships within an age class between dominance index and site fidelity, between dominance index and arrival score, and between dominance index and arrival score were analysed to remove age as a variable. The results are displayed in Table 3.6.7a - c. Within 3rd and 4th/5th cohorts there was a significant negative relationship between dominance index and site fidelity index. That is, more dominant birds were more site- faithful. There were no significant relationships between these variables within 1st and 2nd year age classes.

Arrival score and site fidelity index were significantly negatively correlated within 3rd and 4th/5th year age classes (Table 3.6.7b). Arrival score and dominance index were significantly positively correlated for the 4th/5th year age class but not for any other age class.

Tables 3.6.8a - c summarise the mean $\pm$ 1 s.e. arrival scores, dominance indices and site fidelity indices for each age class as depicted in Figures 3.6.1 - 3.6.3.

Table 3.6.1 Aggressive interactions won and lost by four age classes of chough at Roost 1.

AGE CLASS	WON	LOST	N
4th/5th	115 (79%)	31	146
3rd	133 (69%)	59	192
2nd	82 (40%)	123	205
1st	45 (26%)	131	176

$X^2 = 125.91$ 3 d.f. $p < 0.001$

Tables 3.6.2a - d. Wins and losses in aggressive interactions within four age classes of choughs at Roost 1.

3.6.2.a

AGE CLASS	WON	LOST	N
4th/5th	115	31	146

$X^2 = 48.32$ 1 d.f. $p < 0.001$

3.6.2.b

AGE CLASS	WON	LOST	N
3rd	133	59	192

$X^2 = 28.16$ 1 d.f. $p < 0.001$

3.6.2.c

AGE CLASS	WON	LOST	N
2nd	82	123	205

$X^2 = 8.20$ 1 d.f. $p < 0.001$

3.6.2.d

AGE CLASS	WON	LOST	N
1st	45	131	176

$X^2 = 21.01$ 1 d.f. $p < 0.001$

Table 3.6.3. Aggressive interactions initiated and not initiated by four age classes of choughs at Roost 1.

AGE	INITIATED	NOT INITIATED	N
4th/5th	104 (71%)	42	146
3rd	103 (54%)	89	192
2nd	77 (38%)	128	205
1st	57 (32%)	119	176

$X^2 = 59.02$ 3 d.f. $p < 0.001$

Table 3.6.4. Aggressive interactions won and lost by the bird which initiated the interaction for four age classes of choughs at Roost 1.

AGE	INITIATE & WON	INITIATE & LOST	N
4th/5th	93 (89%)	11	104
3rd	88 (85%)	15	103
2nd	51 (66%)	26	77
1st	29 (51%)	28	57

$X^2 = 39.63$ 3 d.f. $p < 0.001$

Table 3.6.5. Aggressive interactions won and lost by choughs which were settled in a roost site at the start of the interaction for four age classes of chough at Roost 1.

AGE	RESIDENT & WON	RESIDENT & LOST	N
4th/5th	56 (85%)	10	66
3rd	72 (71%)	30	102
2nd	45 (41%)	64	109
1st	25 (25%)	76	101

$X^2 = 77.69$ 3 d.f. $p < 0.001$

Table 3.6.6. Interactions by all age classes of choughs at Roost 1 which involved the three categories of aggressive interaction.

Aggressive interactions			
Passive supplant/ avoidance	Threat	Physical contact	N
212	344	163	719

$X^2 = 73.14$ 2 d.f $p < 0.001$

(based on goodness-of-fit test with equal expected proportions.)

Table 3.6.7a - c. Relationships between dominance index, arrival score, and site fidelity index for each age class of chough at Roost 1.

a. Dominance index correlated with site fidelity index.

AGE	r_S	p	N
4th/5th	- 0.54	< 0.05	14
3rd	- 0.55	< 0.05	13
2nd	- 0.14	n.s.	12
1st	- 0.13	n.s.	14

b. Arrival score correlated with site fidelity index.

AGE	r_S	p	N
4th/5th	- 0.59	< 0.01	26
3rd	- 0.38	< 0.05	27
2nd	- 0.001	n.s.	30
1st	- 0.19	n.s.	18

c. Arrival score correlated with dominance index.

AGE	r_S	p	N
4th/5th	0.55	< 0.05	14
3rd	0.42	n.s.	9
2nd	0.57	n.s.	8
1st	0.25	n.s.	11

Tables 3.6.8a - c. Summary of mean (± 1 s.e.) arrival scores, aggression indices, and site fidelity indices for four age classes of chough at Roost 1.

a. Arrival scores.

AGE	MEAN	s.e.	N
4th/5th	2.12	0.09	26
3rd	2.12	0.05	36
2nd	2.01	0.02	45
1st	1.43	0.07	20

b. Dominance indices.

AGE	MEAN	s.e.	N
4th/5th	0.76	0.08	14
3rd	0.77	0.07	14
2nd	0.41	0.08	14
1st	0.21	0.08	15

c. Site fidelity indices.

AGE	MEAN	s.e.	N
4th/5th	0.22	0.03	26
3rd	0.29	0.03	34
2nd	0.46	0.03	36
1st	0.55	0.03	21

FIGURE 3.6.1

Mean ± 1 s.e. dominance indices of four age classes of chough at Roost 1.

Details of the calculation of dominance index can be found in Section 3.6.2. Sample sizes can be found in Table 3.6.8b.

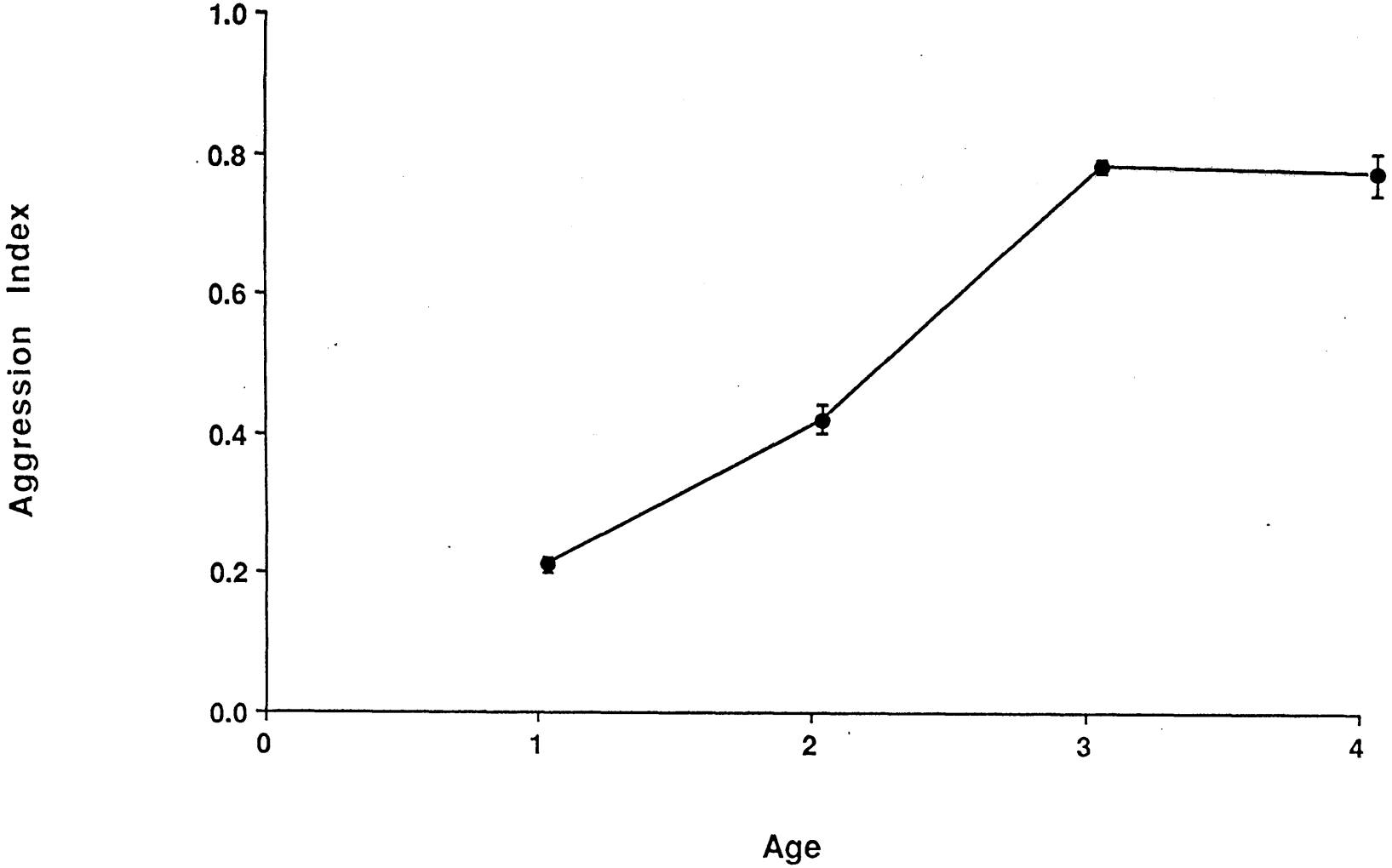

Aggression Index
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
Age

FIGURE 3.6.2

Mean $\pm$ 1 s.e. arrival scores of four age classes of chough at Roost 1.

Details of the calculation of arrival score can be found in Section 3.6.2. Sample sizes can be found in Table 3.6.8a.

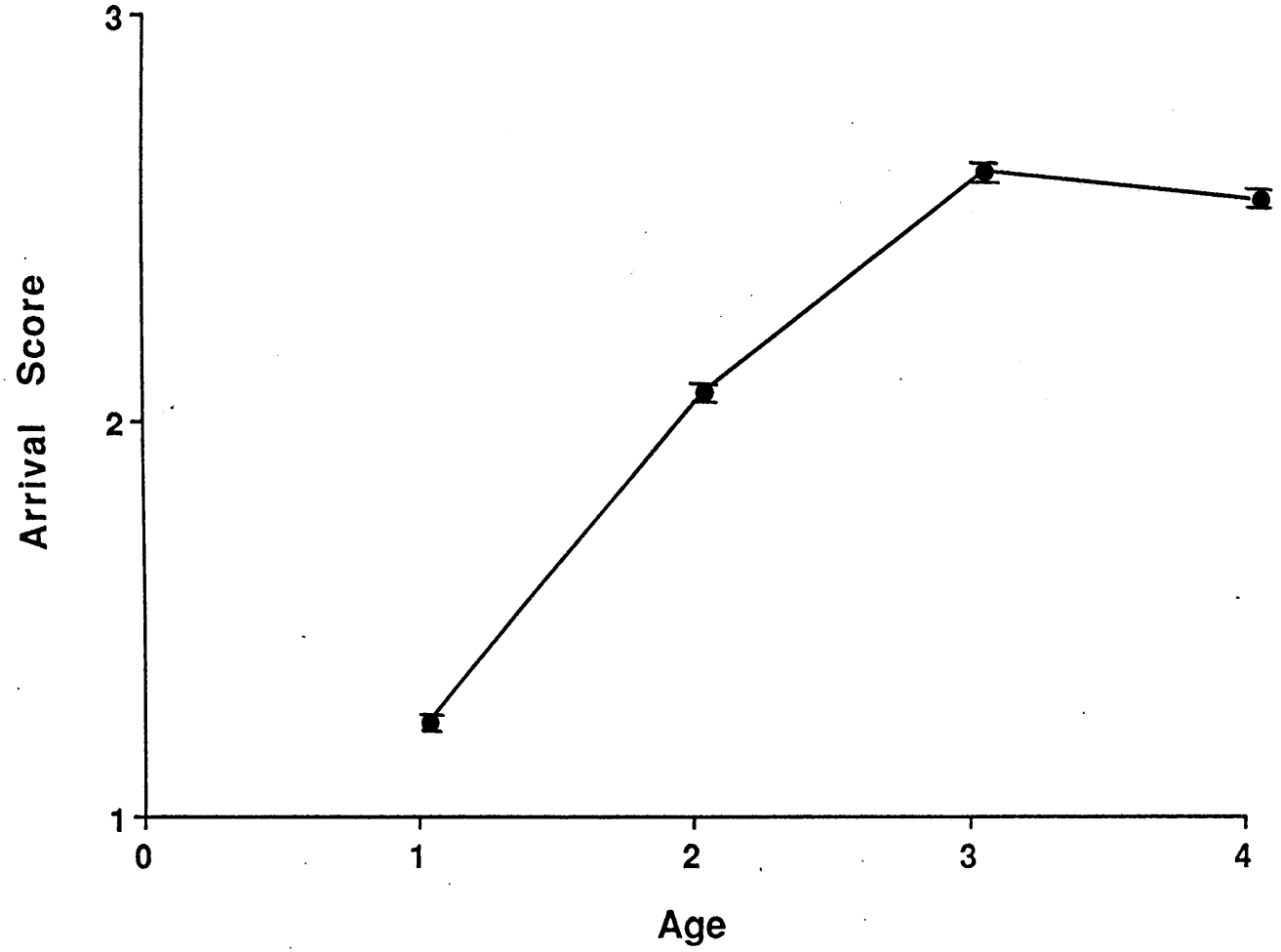
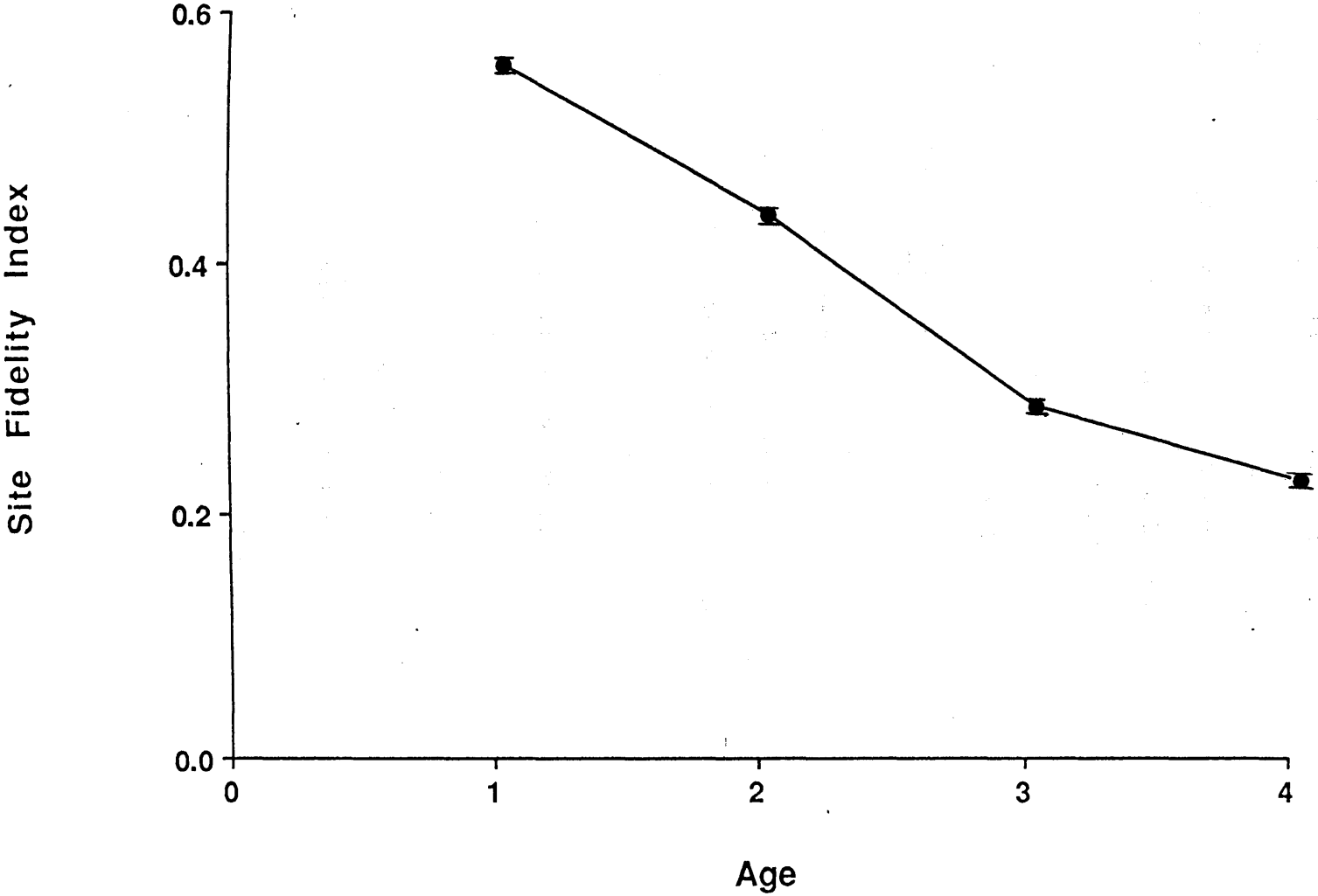

Arrival Score
3
2
1
0
1
2
3
4
Age

FIGURE 3.6.3

Mean ± 1 s.e. site fidelity indices of four age classes of chough at Roost 1.

Details of the calculation of site fidelity index can be found in Section 3.6.2. Sample sizes can be found in Table 3.6.8c.


Site Fidelity Index
0.6
0.4
0.2
0.0
0
1
2
3
4
Age

Spatial organisation within the roost.

Each observation night the second nearest neighbour was recorded for each bird. These data were then combined within each age class and the second nearest neighbours categorised as being the same age or different age. For example, on one night, for twenty 1st year birds, ten out of twenty second nearest neighbours may be of the same age and ten may be of a different age. If, on that night the expectation was that there should only be 6 second nearest neighbours that were also first years (if the distribution was random with respect to age), then the numbers observed are greater than the numbers expected. The number of nights on which the observed frequency of second nearest neighbours of the same or different age was greater or less than expected were totalled for Winter (November - March), Spring (April - June) and Summer (July - October). The results are shown in Table 3.6.9.

There was no significant difference in frequency of second nearest neighbours being of the same greater or less than expected during the winter for all four age classes. This means that there was no clumping of age classes with birds of their own age.

During the spring there was a significant increase in the frequency of second nearest neighbours being of the same age for first and second years choughs. The results for older choughs shows that their second nearest neighbours were no different than expected by chance. Thus there was clumping of first years with other first years and clumping of second years with other second years.

For all age classes during the summer there was a significantly increased chance of a bird having a second nearest neighbour which was the same age. In other words, each age class tended to clump with birds of the same age.

Table 3.6.9. Numbers of observation days when the frequency of second nearest neighbours that were of the same age was less than, and greater than that expected by chance. Data is presented for each age class in three seasons.

WINTER

AGE	NUMBER OF SECOND NEAREST NEIGHBOURS OF SAME AGE: LESS THAN EXPECTED	GREATER THAN EXPECTED	N	SIGN TEST z	
1st	4	8	12	0.87	n.s.
2nd	6	13	19	1.38	n.s.
3rd	9	10	10	0.00	n.s.
4th/5th	5	3	8	0.35	n.s.

SPRING

AGE	NUMBER OF SECOND NEAREST NEIGHBOURS OF SAME AGE: LESS THAN EXPECTED	GREATER THAN EXPECTED	N	SIGN TEST z	
1st	12	40	52	3.74	p<0.01
2nd	13	43	56	3.88	p<0.01
3rd	12	21	33	1.39	n.s.
4th/5th	2	5	7	0.76	n.s.

SUMMER

AGE	NUMBER OF SECOND NEAREST NEIGHBOURS OF SAME AGE: LESS THAN EXPECTED	GREATER THAN EXPECTED	N	SIGN TEST z	
1st	5	50	55	5.93	p<0.01
2nd	11	42	53	4.12	p<0.01
3rd	14	48	62	4.19	p<0.01
4th/5th	18	36	54	2.32	p<0.05

3.6.4 DISCUSSION.

Animals which live in relatively stable social systems often demonstrate recognised dominant - subordinate relationships with their social group members. These relationships are maintained by fights or displays although interchanges of submissive and ritualised aggressive behaviour, non-aggressive displacements and avoidance behaviour probably account for the majority of dominance - subordinance interactions (Kaufmann 1983)

For a dominant - subordinate relationship to remain stable, the submissiveness of the subordinant is crucial. Rowell (1966) stated that too much stress was put on the aggressive aspects of dominance whereas less conspicuous submissive behaviour had been overlooked as playing the major part in maintaining the relationship. Within these relationships it is usually to the advantage of both parties involved to recognise and accept an established dominant - subordinant relationship. This allows both parties to save energy, time and the risk of injury (Clutton-Brock *et al.* 1979). The dominant individual may also win immediate precedence of access to the contested resources. The outcome of aggressive contests between individuals depends on the asymmetries between them (Maynard Smith 1982). Such asymmetries include body size (Krebs & Perrins 1978, Hogstad 1987), accrued experience in aggressive interactions (Arcese & Smith 1985) and prior occupancy (Davies 1978, Yasukawa & Bick 1983, Hogstad 1987, Nilsson & Smith 1988)

Dominance is relevant to natural selection when it accrues increased fitness by allowing access to necessary limited resources such as food, water, roost sites, or receptive mates. In other cases, dominance rank can not be related to any of the above resources (Bernstein 1970) as in some primate societies.

Dominance within an avian roost may not only be accounted for by competition

for the resource (in this case roost sites) but may also be a means of establishing and maintaining a hierarchy for the future (next day or period of time while the group is cohesive) when the birds are feeding. This allows more time to be spent feeding and less time involved in aggressive, time-consuming interactions.

In the case of roosting choughs birds which initiated interactions were more likely to win. This suggests that there was recognition of dominant - subordinant relationships (Table 3.6.4). The probability of initiating and winning such initiated interactions was lower in younger birds, especially newly fledged birds, which suggests that they still had to recognise or learn which birds were dominant (Arcese & Smith 1985). The results in Table 3.6.6 indicate that birds become involved in actual physical contact comparatively infrequently. Disputes were settled by passive supplantation / avoidance and by threat. This argues that birds can learn and recognise dominant - subordinant relationships thus avoiding costly physical interactions (Parker 1974, Maynard Smith 1982).

In cases where there is no obvious limiting resource, dominant individuals may give way to lower ranks (Kaufmann 1974). Fitness benefits, relative to increased dominance, however, may often be difficult to demonstrate. Dominance may increase fitness in other ways such as allowing the offspring of dominant individuals to experience a greater resource access when young and thus increased survival. Few data from this study are available to test such hypotheses. However, in the case of one newly fledged colour ringed chough with an identifiable colour ringed female parent with an dominance index of 1.00 (i.e. never seen to lose an aggressive interaction, and therefore a dominant bird), the offspring also had a high aggressive index (1.00) and maintained its roost site close to its parents (pers. obs.). In fact, on one occasion, this juvenile was seen to aggressively displace its dominant female parent from its roost position. This observation, however is open to other interpretations although the interaction was relatively aggressive and involved much

physical contact between the two birds. The interaction was not a failed food-begging attempt, with the parent moving away, as no begging calls were heard which accompany such interactions. This juvenile also won all interactions against older birds which had been resident in the flock for much longer.

Dominance hierarchies are also more likely to develop in conditions where there is a lack of opportunity for subordinates to escape. Dispersal by subordinates, especially young ones, is a common response (Butler 1980, Ekman *et al.* 1981, Ekman 1987). Subordinate individuals may have to assess the advantages and disadvantages in remaining in a situation where escape would prevent them from obtaining at least some of the advantages associated with remaining with dominants. The disadvantages in moving to a situation where there is less aggression may be a reduction in what is to be gained by remaining with dominant birds. One advantage may be increased food finding opportunities (Weatherhead 1983).

One alternative strategy to subordinate birds moving away entirely from a communal roost where there are numbers of dominant birds and aggression levels may be high, is to roost close to other young birds whose dominance index may also be low. In this way, young birds may retain any advantages of roosting within a larger group (many of whose members may be more dominant) . At the same time they may experience less aggression by roosting with other birds of low dominance status (i.e. other young birds).

Younger birds had a lower site fidelity index than older birds so, although they were more mobile within the roost, they still maintained close contact with other birds of the same age. For older birds the advantages of roosting close to other dominant birds are more difficult to establish.

Clumping by birds of the same age only occurred during the spring and summer as numbers at the roost increased, (see Figure 3.2.2). It may be that, as numbers

increased there was more competition for suitable roost sites and therefore more aggression shown to younger birds, especially during the post-fledging period. There was not enough data on sibling groups to tell whether part of the clumping by first years was due to siblings roosting together, although this did occur (pers. obs.).

The clumping of older birds during the summer is more difficult to explain. As numbers increase at the roost the sheer numbers of other birds may cause older birds to resort to one favourable roost area. With other dominant birds surrounding them the incidence of interactions which each dominant bird experiences may be lower as younger birds may be less likely to enter an area with a high proportion of dominant birds. One may have expected to find a lower degree of clumping or even repulsion between older birds due to their relatively high dominance ranks. However within this group of older birds one may expect variation in dominance index. Breeding birds returning to the roost with or without young or birds returning after a failed breeding attempt may have to adjust their levels of territoriality for this clumping to occur, although it is uncertain as yet as to how territorial choughs are around their nest site. From personal observation breeding birds will chase off others, especially other neighbouring pairs while at the same time allowing non-breeding flocks to feed within the area around the nest site. As a proportion of fourth and fifth year birds are returning breeders it seems feasible to suggest that some alteration of their territoriality must occur for them to roost close to other returning breeders.

Establishment within social groups may be crucial to an individual's probability of surviving its first winter as is the case for willow tits *Parus montanus* (Ekman *et al.* 1981). However, Marsh tits *Parus palustris* do not normally leave a social group even if weather or feeding conditions deteriorate markedly during winter (Gibb 1954, Perrins 1979, Nilsson & Smith 1988).

Prior residency in social feeding groups has been shown to determine dominance status (Perrins 1979), in magpies (Eden 1987) and in willow tits (Hogstad 1987). For willow tits, in winter ranges with both adults and juveniles, adults always dominated juveniles although, since adults had been established for at least a year, this could depend on either their earlier residence or their greater age. In interactions between resident juveniles and trespassing adults, adults lost. In the case of roosting choughs, even though young birds were resident in a roost site, they lost the majority of aggressive interactions with other birds even though they were established in the social roosting flock.

Older choughs initiated more interactions in which they were involved than younger birds. The fact that they also won more of the aggressive interactions they initiated suggests that dominant birds initiated more of the interactions they were involved in. Young birds in relatively high density roost flocks may not always be able to avoid aggressive interactions. Young choughs in this study were observed being displaced from one roost site and pushed towards other roosting birds. This caused further aggression to be directed toward them. In these cases the displaced bird was not regarded as initiating an interaction as it had been involuntarily placed in that situation due to its earlier displacement. This intrusion into the individual space of a second roosting bird may have been seen as a threat (Kaufmann 1983) and caused an ensuing aggressive interaction. On several occasions newly fledged choughs have been observed in this situation. It may be that they have yet to learn to avoid entering other birds individual spaces and to learn avoidance tactics. Also at this early stage their flight manouverability is poor and avoidance may be difficult. In such circumstances, one alternative strategy for these young, subordinate birds is to roost where they can avoid such aggressive interactions, such as in low density areas or areas away from dominant birds (Still *et al.* 1987). This has also been observed in rooks, Swingland 1977), red-winged blackbirds

(Weatherhead & Hoysak 1984) and starlings (Summers *et al.* 1987).

Although site fidelity, dominance index and arrival score were all significantly correlated with age, when age was removed as a variable, site fidelity index was significantly correlated with dominance index for 3rd and 4th/5th year birds only. Young birds may therefore take time to establish sites.

For young choughs arriving early to the roost one may suggest that this accrues the advantage of finding and settling into a roost site. However, no advantage is gained in arriving early and settling in a roost site as, for young birds, (1st & 2nd years), site fidelity is not correlated with arrival score.

Fourth and fifth year birds, which were more aggressive, arrived later to the roost. This may imply that they could easily displace other birds which were already settled. Valuable time did not need to be spent before dusk in establishing a roost site. These birds could therefore presumably spend more time in undisturbed maintenance activity or feeding before settling into a roost site.

Aggressive interactions within roosts have been observed in many avian species eg. starlings (Feare 1984), black vultures *Coragyps atratus* (Rabenold 1987), red-winged blackbirds (Weatherhead & Hoysak 1984) although very little aggressive behaviour was noted among white wagtails *Motacilla a. alba* in Israel and Pied Wagtails *M. a. yarrellii* in England (Zahavi 1971a). In this case roosts were not in one traditional site but moved from night to night. Low levels of aggression may suggest that the aggressive maintenance of roost sites was not as important as sites changed from night to night or that dominance hierarchies were established and maintained while feeding.

In general, roosting dominant-subordinate relationships and site selection

strategies can give an insight into the advantages and disadvantages of communal roosting accrued to individual birds within the flock. Dominant birds can maintain preferred, higher quality roost sites, which may be microclimatically, anti-predator or socially superior. Low ranking birds may trade off increased aggression, the need for avoidance behaviour and increased chances of predation (caused by peripheral roosting) with the advantages they may receive from increased food locating chances due to roosting with dominant and superior foragers. Another advantage of flocking and communal roosting by non- breeding birds may be increased probability of finding a mate (Baeyens 1981, Birkhead & Clarkson 1985, Birkhead *et al.* 1986).

In summary:-

Older choughs (3rd and 4th/5th years) won a higher proportion of aggressive interactions than younger choughs.

Older choughs initiated a larger proportion of the aggressive interactions in which they were involved than did younger choughs.

Older choughs won a higher proportion of aggressive interactions which they initiated than young choughs.

Young choughs which were resident in a roost site lost a greater proportion of aggressive interactions than older resident choughs.

There were significantly more passive supplantations/avoidances and threats and fewer physical contacts during aggressive interactions than an expected equal ratio.

Older choughs arrived at the roost later relative to young choughs.

Young choughs were less faithful to a roost site than older choughs.

For each age class in summer, a higher proportion of second nearest neighbours were of the same age than expected by chance (i.e. Birds tended to roost with others of the same age.

There was no segregation of age-classes in winter and only for 1st and 2nd years in the spring.

3.7 THE ROOST AS A CENTRE FOR "INFORMATION TRANSFER" (TESTING THE "INFORMATION CENTRE HYPOTHESIS")

3.7.1 INTRODUCTION.

The previous findings at the roost have shown that the roost is not an amorphous gathering of birds but an organised system, the social structure being effected through a dominance hierarchy and the maintenance of roosting positions on the cliff by birds relative to their age and dominance.

Many authors have noted an association between sociality and patchily distributed, unpredictable food resources (Fisher 1954, Crook 1965, Lack 1968, Alexander 1974, Evans 1982a,b). To explain this association, Ward and Zahavi (1973) suggested that birds in such assemblages have the opportunity to gain information from each other about the locations of these patchy, ephemeral feeding sites. This suggested function of communal roosting does not explain why birds roost preferentially in parts of the roost which may reduce predation risks, while the subordinate birds occupy the less favoured positions. Weatherhead (1983) suggested the two strategy hypothesis which proposes that, at a roost, birds are not equal in their food finding abilities with the subordinate birds being less able to find or defend good sites. He suggested that there are advantages to dominant birds roosting with subordinates as they are buffered from predation by the presence of subordinate birds which roost on the periphery of the flock where the probability of predation is higher. The subordinate birds will tolerate this as they can parasitise the dominant, more skilled, feeders by obtaining information on the location of good feeding sites, thus eliminating the costs of sampling the environment themselves. The method which the subordinate birds, or "followers", use to obtain this information, (presumably by determining which birds have

foraged successfully when they return to the roost), is debatable.

Andersson *et al.* (1981), Brown (1986) and Greene (1987) tested the "Information Centre" hypothesis using breeding colonies of birds with results supporting the hypothesis. However, colonial breeders differ from roosting flocks in that birds at a breeding colony have many opportunities within a day to identify and follow successful feeders purely on the basis of observing food brought back to the young at the colony. Drawbacks occur in using return visits or success as colony return frequencies depend on feeding site to colony distances; as these distances increase, the return frequencies decrease (Nelson 1978). Theoretically, unsuccessful birds may be identified as returning to the colony with less food to feed their young than successful birds. This however could also occur between parents with different numbers of young or between broods which differ widely in age (development) and therefore food requirements (Bayer 1982)

Members of roosting flocks, however, do not have the advantage of seeing food brought back to the roost by othersand must have an alternative method of identifying successful foragers. That information transfer at a communal roost occurs has never been definitely proven.

The experimental design necessary to investigate information transfer at roosts is quite straightforward, involving the placing of rich food patches remote from the roost. The number (N1) of birds at the patch is counted during the foraging period in which the patch is discovered. This number, N1, is compared with the number of birds (N2) finding the bait during the next foraging period where the birds have visited the roost in the intervening period. If N2>N1 this suggests that information transfer is occurring although this result is possible by chance too. As the food patch is discovered by chance initially, chance should result in some birds also

finding the patch independently during the second foraging period. Numbers will therefore increase if the original finders return to this same foraging patch.

If information on food patches is being transferred then one may expect the recipients of this information to make use of it at the first opportunity ie. by following at the very start of the second foraging period. Therefore, N2 should only be considered as the number of birds finding the patch at the outset of the second foraging period. If N2=N1 this suggests that no information transfer is occurring. This interpretation however, is too simple. It is possible that the finders of food-patches were not followed back to the experimental feeding sites as food was abundant elsewhere and the information not needed by other roost members. If N2<N1 then the experiment has failed because not all the birds that discovered the food patch returned to it. This may be because the experimental food patch was not as rich or as suitable as the available natural food sources. This should be assigned as a failed experiment and not the negation of the existence of information transfer, (Weatherhead 1987).

There are seven components or requisites to the information transfer mechanism. If unsuccessful birds fail to participate in any or all of the three or four final components, information transfer can be rejected as taking place. The seven components are as follows:

1. Individuals which have fed well at one site frequently return, (Kiss & Moller 1986, Waltz 1987), thereby possessing information that may be acquired by others.
2. All members of a roost/colony do not have equal foraging success within an given time period.
3. Unsuccessful birds must be able to detect successful individuals.
4. Unsuccessful individuals must leave the colony/roost with, or soon after, a

successful individual has left i.e. synchrony of departure.

5. Unsuccessful individuals follow successful feeders.
6. Toleration at the feeding site must happen otherwise there would be no reason for unsuccessful birds to follow to these sites if they cannot then participate.
7. The unsuccessful birds foraging efficiency must improve sufficiently to gain a net benefit in participating in the whole process.

This is examined in more detail by Mock *et al.* 1988.

Although Loman & Tamm (1980) produced moderately positive evidence of information transfer in roosting birds, their experimental technique and interpretation of results give rise to query. They chose the first day of an experimental trial as the day on which the food patch was put out and not as the day on which the birds, (in this case hooded crows *Corvus cornix* and ravens *C. corax*) found the food patch. Therefore, they included in their analyses trials on which the food patches were not found. These trials should have been regarded as failed trials.

Kiis & Moller (1986) conducted sixteen trials using greenfinches, (*Carduelis chloris*). In nine trials the food patches were found and, of these trials, eight gave the result N2<N1. The remaining trial produced the result N2=N1. These results should be regarded as failed trials and not as evidence against information transfer. The results of their study support the interpretation that the experimental food patches they provided were of poorer quality than the natural food sources available at that time to the greenfinches.

The structuring of the communal chough roost (Still *et al.* 1987) and the dominance hierarchy found in this study suggested that there were advantages to birds using the roost as suggested by Weatherhead (1983) and that information on feeding sites could be a reason for choughs roosting together. Young birds are

poorer feeders (described later in Section 4.4) and experience more aggression than older birds. The advantages to these young birds in roosting with older, dominant, and more experienced foragers may be ones of increased foraging success using information accrued at the communal roost. As a result, it was decided to test the "Information Centre" hypothesis.

3.7.3 METHODS.

Only colour-ringed birds were used in the analyses as it was thus possible to distinguish which individual birds found on the bait on Day 1 and returned the next day and also which new birds arrived at the bait on Day 2. The use of colour-ringed birds in this experiment therefore has advantages over all previous experiments of this kind as more detailed data can be obtained. All experimental food patches were placed within the area used by choughs attending Roost 1.

The experiment took place between 18.1.88 and 12.2.88 i.e. during the winter when birds have the shortest time in which to find food due to the constraints of day length. The experiment was composed of eleven trials each covering a period to two days in which 25 m^2 areas were baited with 250g of mealworms. The bait sites were located in sand-dune systems in sites which could not be seen from the roost. Distances from the roost to food patches varied from 1 km to 2 km. The bait was placed on the ground before the choughs left the roost in the morning and observed from at least 50 m. On the first day of a trial (Day 1), the baited patch was watched continually for the duration of the day: the time of arrival and identity of all colour-ringed choughs finding and feeding at the bait were recorded. On the second day (Day 2), the bait was replenished at the same location before the birds left the roost and the site observed for the first hour after the roost was vacated. Again, the arrival times and identity of all colour-ringed birds finding and feeding at the bait were recorded.

Of the eleven trials started, two were aborted after Day 1 as no choughs found

the bait. Of the remaining nine trials, three others were aborted as the bait was taken by gulls (*Larus* spp.). The bait could not be replaced in the same location as the gulls were quick to return to the site. The six remaining trials were rotated over four locations to prevent the choughs from learning to return to the same site for food. Sites were used again after a minimum of eight days. Also, if the bait was seriously depleted by the choughs during the course of Day 1, more was placed in the same location but only during such time as there were no choughs in the vicinity to prevent human disturbance.

3.7.3 RESULTS.

i) *Time taken to find bait and numbers finding bait on Day 1.*

Birds took several hours to find the bait and, even after finding the bait, numbers did not increase until 6 hours after the bait was placed out (Figure 3.7.1). Numbers shown in Figure 3.7.1 only deal with colour-ringed birds so that the arrival of new birds could be distinguished from the possible return several times of the same birds. Although the mean cumulative number of colour-ringed birds at the bait was under two until after six hours, the actual number of birds overall may have been higher since not all birds were colour-ringed. In most cases the bait was first found by paired birds, only one of which was colour-ringed. There were no cases of flocks larger than two being first to find the bait on Day 1.

ii) *Time of arrival of the first bird to the bait.*

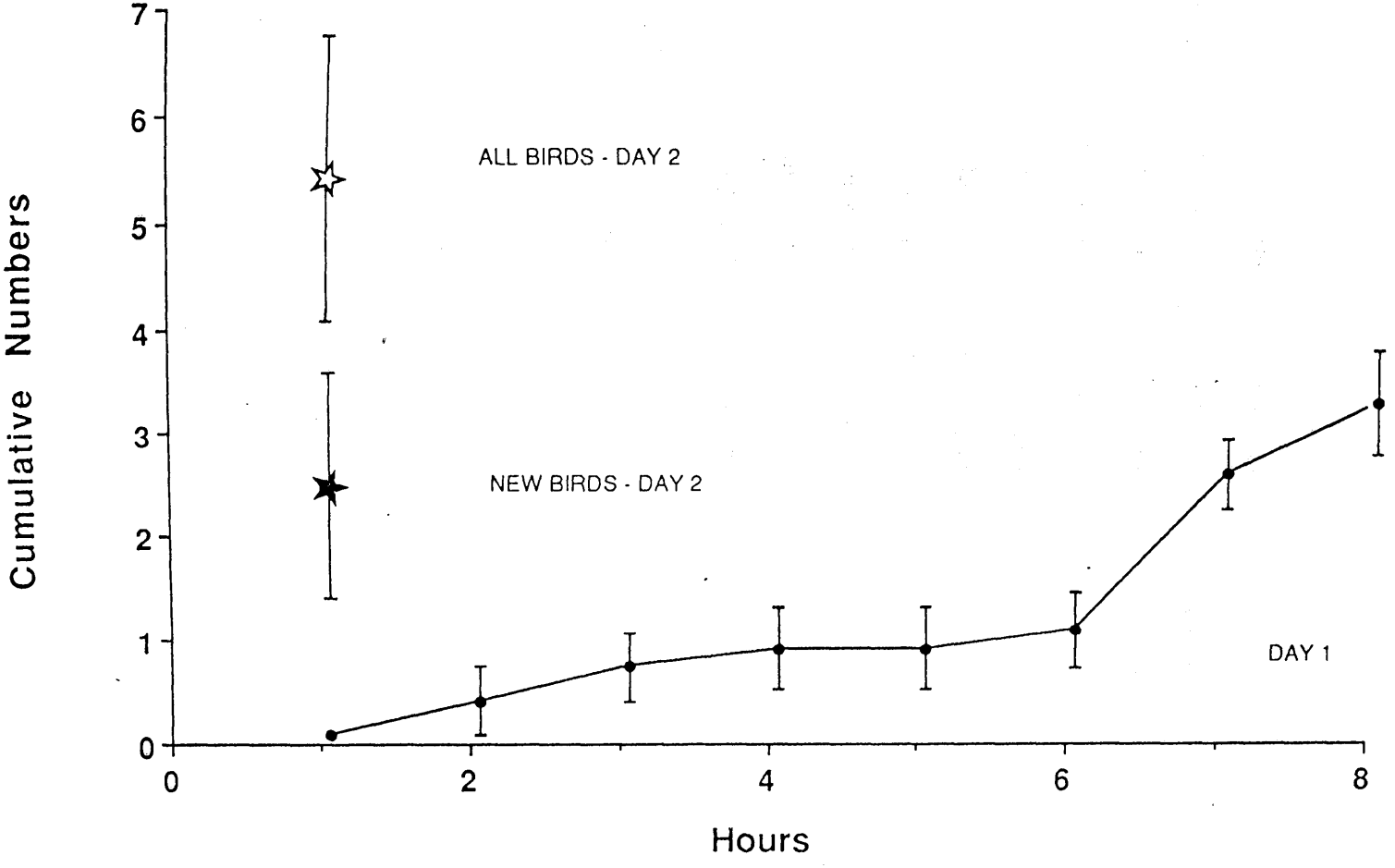
The data used in this analysis are for the time of arrival of the first bird regardless of whether it was colour-ringed or not. In all cases except one, the first bird to arrive at a bait site was in fact colour-ringed.

Figure 3.7.2 shows the mean $\pm$ 1 s.e. time taken over the six trials for the first bird to arrive at the bait after leaving the roost on Day 1 and on Day 2 based on

FIGURE 3.7.1

Mean (± 1 s.e.) cumulative numbers of colour-ringed choughs arriving at bait sites on Day 1 of "Information Centre" experiment. Also shown are the median total numbers of colour-ringed choughs arriving at the bait sites in the first hour of Day 2 and the mean (± 1 s.e.) of "new" colour-ringed choughs arriving in the first hour of Day 2.

Sample size in all cases is 6 (i.e. 6 bait experiments).


Cumulative Numbers
7
6
5
4
3
2
1
0
ALL BIRDS - DAY 2
NEW BIRDS - DAY 2
DAY 1
0
2
4
6
8
Hours

all six trials. The mean ± 1 s.e. are used to show the range in the data. Statistical analysis used the sample medians. There was a significant difference in the median arrival time on Day 1 compared to Day 2. The median arrival time on Day 1 was 242.5 minutes and on Day 2, 7.00 minutes.

iii) *Do finders return to the bait the following day?*

As mentioned above in the introduction, Kiis & Moller (1986) found that birds in half their experimental trials did not return to the food patch on the following day. This was possibly because the food patch was of poorer quality than food which the greenfinches could find elsewhere. As a check that this was not happening during this experiment with choughs, the probability of a bird returning on the second day was calculated. Of the eighteen colour-ring sightings at the bait, there were seventeen return visits the following day i.e. a probability of 0.94 of a bird returning. This result does not include any return visit made more than once during the second day by any individual bird.

iv) *The arrival on Day 2 of "naive" or new birds which did not find the bait on Day 1.*

To compare the number of birds finding the bait on Day 1 and Day 2, only the numbers arriving in the first hour of each of the two days are used. New birds were assumed to make use of any information they may possibly receive at the roost at the start of the second foraging period as explained above. Therefore, the figure of one hour observation at the bait on Day 2 was arrived at to cover only this period when it was assumed the new birds would turn up. The choice of one hour observation was also a means of comparing the numbers of birds on the bait in the first hour of Day 2 with the numbers in the first hour of Day 1. This can give data to indicate the speed at which birds arrived at the bait giving further indication as to whether birds have learned of the location of a food patch (see Figure 3.7.2).

FIGURE 3.7.2

The mean time (minutes after dawn, $\pm$ 1 s.e.) for colour-ringed choughs to find the bait patches on Day 1 and Day 2 of the "Information Centre" experiment.

Sample size in both cases is 6 (i.e. 6 bait experiments).

Mann-Whitney U-test $U_1 = 0$, $p < 0.05$

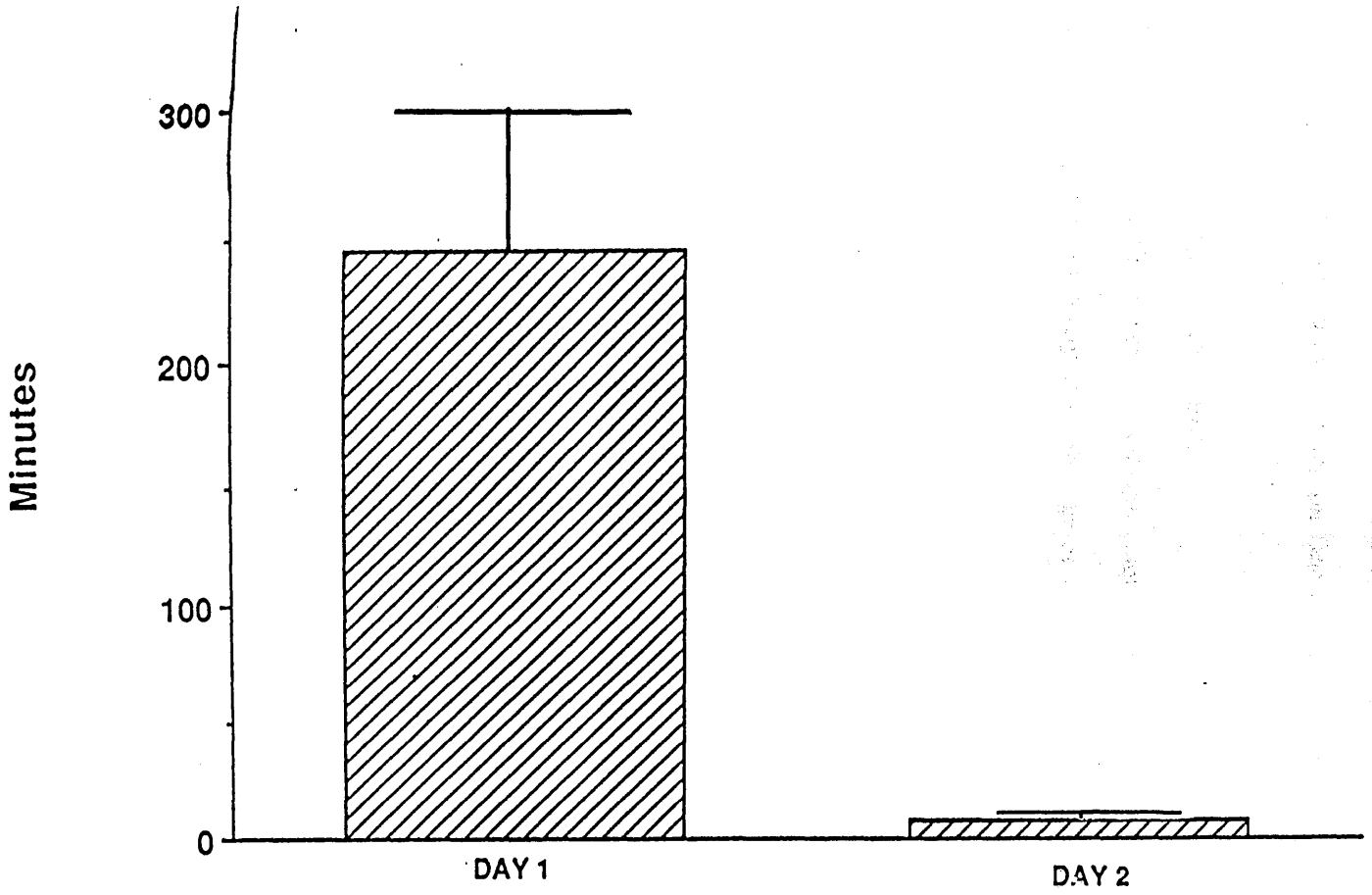

Minutes
300
200
100
0
DAY 1
DAY 2

Figure 3.7.3 shows the mean ± 1 s.e. numbers of of colour-ringed birds arriving at the bait in the first hour of Day 1, the mean ± 1 s.e. total number of arrivals on Day 2 (first hour), and the number of this total which is comprised of new birds which were not present on Day 1. The means ± 1 s.e. are used to show the range of the data. Statistical analyses used the medians. Significantly more birds arrived in the first hour of Day 2 than arrived in the first hour of Day 1 for both the median total and median "new" birds arriving on Day 2.

v) *The identity of the "new" birds.*

Unfortunately there were not enough colour-ring sightings at the bait to provide data to carry out any analyses of the age or status of new birds arriving at the bait on Day 2 as few relative to the total colour- ringed population found the bait.

vi) *Do new birds (followers) roost near finders?*

The roosting positions of colour-ringed choughs at the communal roost (Roost 1) were recorded on the evening of Day 1 of a trial. The distances between each "follower" on Day 2 and the nearest "finder" to it were measured. As a comparison, the distances were also measured between followers and the nearest colour-ringed bird which was neither a finder or a follower during a specific trial i.e. a non-participant. The results are shown in Table 3.7.1. There was no significant difference in the median roosting distance apart between followers and finders and follower and non-participants. Followers did not roost closer to the birds which they followed than to non-participants.

As a means of checking this by a different method, the distances were measured between finders and their nearest follower, and between finders and their nearest non-participant. The results are shown in Table 3.7.2. Again, there was no significant difference in the roosting distances apart between finders and their nearest follower and finders and their nearest non-participant.

FIGURE 3.7.3

The numbers of colour-ringed choughs arriving at the bait in the first hour of Day 1, the mean ($\pm$ 1 s.e.) total number ("All") of colour-ringed choughs arriving in the first hour of Day 2 and the mean ($\pm$ 1 s.e.) number of "new" colour-ringed choughs arriving in the first hour of Day 2 of the "Information Centre" experiment.

"New" birds were colour-ringed birds which were not sighted on the bait on Day 1. "All birds" is a combination of "new" birds and birds which returned to the bait on Day 2 after finding the bait on Day 1.

Sample size in all cases was 6 (i.e. 6 bait experiments).

Mann Whitney U-test

Day 1 vs. Day 2 ("All") $U_2 = 0$ $p < 0.05$

Day 1 vs. Day 2 ("New") $U_2 = 6$ $p < 0.05$

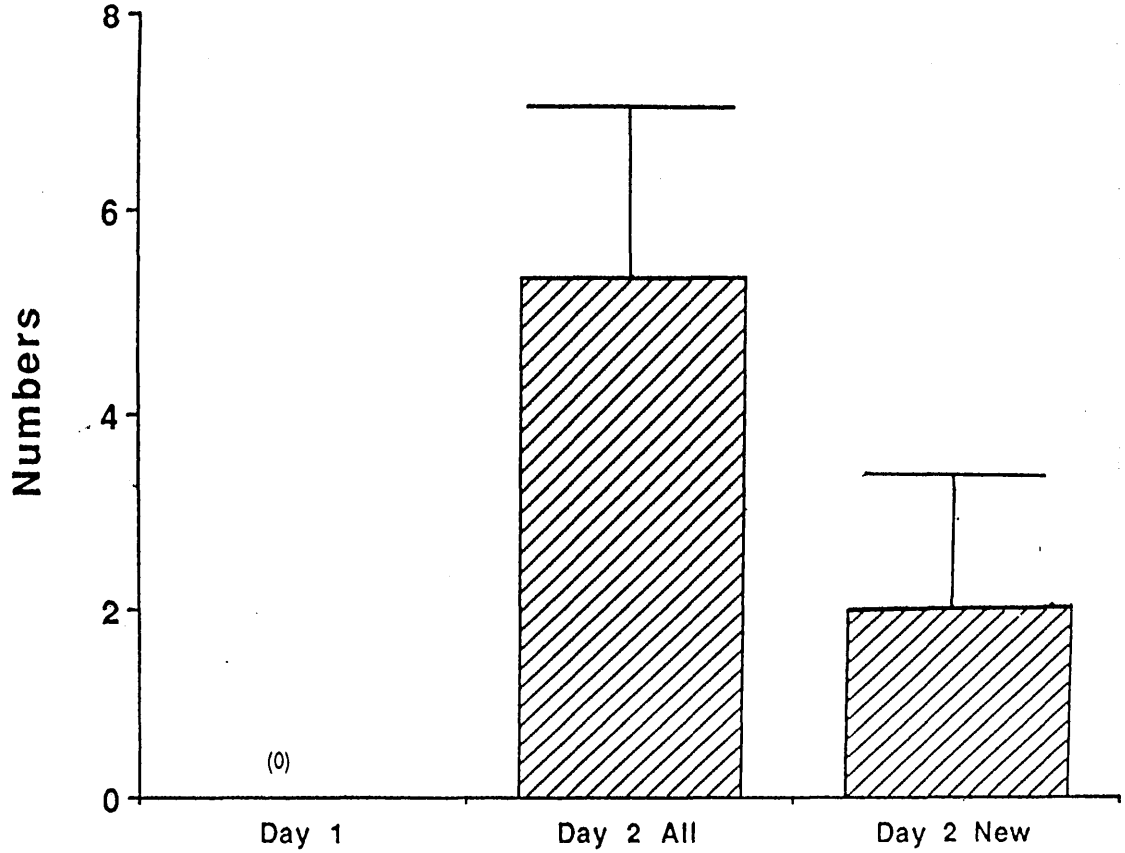

8
6
4
2
0
Numbers
(0)
Day 1
Day 2 All
Day 2 New

Table 3.7.1. Median roosting distance apart (m) between follower and nearest finder and between follower and nearest colour-ringed non-participant, for choughs in the "Information Centre" experiment (see text for details).

	FOLLOWER / FINDER	FOLLOWER / NON-PARTICIPANT
MEDIAN DISTANCE	4.4	4.2

Mann-Whitney U-test N1=12 N2=12 U_1 = 76.5 n.s.

Table 3.7.2. Median roosting distance apart (m) between finder and nearest follower and between finder and nearest colour-ringed non-participant, for choughs in the "Information Centre" experiment (see text for details).

	FINDER / FOLLOWER	FINDER / NON-PARTICIPANT
MEDIAN DISTANCE	6.0	2.0

Mann-Whitney U-test N1=11 N2=11 U_1 = 70.5 n.s.

3.7.4 DISCUSSION.

The above experiments would suggest that information transfer is occurring at the communal roost only if the number of birds arriving at the experimental feeding site is higher at the start of the second, post roosting foraging period than during the first foraging period. The results from Figure 3.7.2 indicate that birds are arriving much faster at the bait on Day 2 than on Day 1, and that the numbers arrived consisted of finders accompanied by new birds. This suggests that information transfer may be occurring between birds. The results from Tables 3.7.1 and and 3.7.2 show that the birds which follow the finders are roosting no closer to them than are any other ringed birds. This suggests that birds do not necessarily gain information from the birds which they roost close to i.e. a bird does not have to be in close proximity to another bird for information to be transferred. This may mean that the information gained is not about details of individuals which can only be ascertained through relatively close roosting distances. Such information may relate to body condition or subtle behaviour associates with a bird which has fed successfully during the day.

It may be that the transfer of information is occurring not when the birds are actually at the roost but as the birds leave the roost in the morning. It is possible that birds are able to watch the movements of others as they fly from the roost and distinguish behavioural patterns associated with birds which were successful feeders on the previous day. One suggestion is that birds follow others which fly from the roost in a purposeful manner and fly directly to a certain location landing in a direct or unfaltering manner. Bayer (1982) poined out that "purposeful" birds may not be good leaders for unsuccessful birds to follow profitably. A purposeful bird actually may have been unsuccessful and, by leaving a colony or roost purposefully, it could maximise its chances of finding a good feeding site quickly by searching independently or by being attracted to feeding flocks or other flying birds. Another reason for being hesitant at defining purposeful birds as being successful feeders is

that the purposeful bird may not actually be going to a feeding site but to a day roost (Burke & Broom 1970, Nelson 1975) or bathing or loafing site (Brown 1958). Purposeful birds may be going to a feeding territory (Taylor 1979) in which cases followers may be excluded from the feeding site.

Another problem with experiments like this is that it is possible that birds are attracted to a food site by the presence of feeding birds (i.e. local enhancement). Even so, if departing from a communal roost with conspecifics increase the chances of local enhancement, then communal roosting could increase food finding chances even without information transfer occurring within the roost.

For the chough whose food source may change with season or climatic changes, it seems likely that one of the advantages of communal roosting may be the increased opportunity for food location. This is not to say that this may occur all year round and all of the time. Communal roosting may be a form of insurance against infrequent food shortages. Some choughs may derive more benefit from this such as young birds who arrive at the communal roosts after fledging. For them, the advantages may be those of learning where the good feeding sites are when they are new to an area.

This experiment showed that birds which find good food sources are quick to return the following day and suggests that choughs are opportunistic feeders, quickly taking advantage of newly appearing food sources. As this experiment was conducted during the winter months when choughs may be stressed to find food (at the time of the experiment there were night frosts and often snow coverage on the ground), the fact that birds returned so readily the following day suggests that easily accessible food was difficult to obtain elsewhere. This supports the view held by some (Holyoak 1971, Roberts 1985) that cold winters may cause higher mortality due to a lack of available food.

For their future conservation, it may be important that choughs are able to find roosting sites which can hold a relatively large number of birds and near an area suitable for feeding. The larger the roost, presumably the greater the chances of a chough being able to take advantage of the behaviour of other choughs either at the roost, or more likely as they leave the roost in the morning. This may be far more important to young choughs if they are new arrivals at a roost, not just in terms of learning from day to day of the best feeding areas, but also learning from season to season the habitats and areas which are the best feeding locations as the type and availability of food changes.

As to further work on this subject, it would be ideal to repeat the experiment at a time when there is a larger number of choughs using the roost and with a higher proportion colour-ringed. The experiment should also cover a longer period to take into account day to day variables such as weather and disturbance. As the experiment was only successful on six occasions, any variation in these factors may bias the data overly. These improvements would give more detailed information on individual choughs which would suggest whether there is any consistent strategy that individual choughs use dependant on their social status and foraging ability.

3.8 ROOSTING BEHAVIOUR AND ENVIRONMENTAL CONDITIONS.

3.8.1 INTRODUCTION.

Herbers (1981) stated that for diurnal animals, time was an important resource; the time available for activities such as foraging was constrained by day length and the constraint of day length could vary seasonally. The proportion of time an animal spends on activities such as feeding and resting, (roosting in this case), may give an indication of pressures such as food availability or foraging efficiency which might affect the animal. One may suggest that if there is a constraint on an activity such as foraging, then a lesser proportion of day time (for diurnal animals) will be spent in activity such as roosting.

The effect of conditions which may influence the roosting behaviour of diurnally feeding birds has been studied by many authors with particular reference to light intensity, wind speed, temperature, cloud cover and time relative to sunset (Brown 1946, Seibert 1951, Davis 1955, Jumber 1956, Meanley 1956, Gurr 1968, Schnell 1969, Davis & Lussenhop 1970, Siegfried 1971, Krantz & Gauthreaux 1975, Broom *et al.* 1976, Swingland 1976, Fleming 1981, Zammuto & Franks 1981, Rees 1986, Warkentin 1985). However, most of these studies have dealt with large and conspicuous congregations of communally roosting birds with little work being done on more solitary roosting species or small congregations (but see Schnell 1969 and Warkentin 1985).

3.8.2 METHODS

All the observations were carried out at Roost 1. Light intensity readings were taken using a photographic photometer and the time recorded when it was estimated

that a) 50% of the roost flock had arrived at the roost and b) 50% had settled on the roost cliff. Similar methods were used by Davis (1955), Swingland (1976), and Brodsky & Weatherhead (1984). Davis (1955) found that the time by which 50% of the birds had arrived was the time least influenced by chance variation. The 50% level was used in this study as opposed to the arrival of the first chough as, in the summer months, choughs often visited the roost during the day time and it was thus difficult to judge if an early arrival by a chough was an intention to roost or a visit to the roost while feeding. The estimated 50% level was derived from counts of choughs at pre-roost gatherings or communal flights around and above the roost before they landed. Two main pre-roost gathering sites were used by the choughs; one in a field and sand-dune area below the roost and one on top of the roost cliff itself.

3.8.3. RESULTS.

Figure 3.8.1 and associated table (Table 3.8.1) show the mean monthly light intensity when 50% of the roost flock had arrived at the roost and when 50% had settled on the cliff. The mean monthly light intensities at the time of 50% arrival and 50% settling depicted throughout the year. Light intensity at arrival time is higher in the summer months than in the winter although light intensity at settling time varied less.

Figure 3.8.2 and associated table (Table 3.8.2) show the mean monthly difference in a) light intensity and b) time when 50% arrived and 50% settled. The difference between arrival time and settling time was higher in the summer months than in the winter. The same pattern was seen in light intensity differences.

Figure 3.8.3 and associated table (Table 3.8.3) show the mean monthly arrival

and settling times calculated as minutes before sunset. Local sunset times were taken from Whitackers Almanac for Glasgow and 8 minutes added to account for the longitudinal difference between Islay and Glasgow (0.0869 minutes added to sunset time per mile west).

Figure 3.8.4 shows the association between day length and light intensity at which 50% of choughs had arrived at the roost. There was a significant positive correlation between increasing day length and light intensity at which 50% of birds had arrived. There was also a significant positive correlation between day length and the light intensity at which 50% of choughs had settled in the roost (Figure 3.8.5). Covariance analysis showed that the slopes of the regression lines of light intensity at arrival and settling time plotted against day length (Figures 3.8.4 and 3.8.5) were significantly different ($F_{1,379} = 60.53$ $p < 0.001$). This demonstrates that the difference in light intensity between arriving and settling was not constant but depended on day length i.e. as day length increased, the light at which birds arrived increased to a greater extent than the light intensity at settling time.

The time before sunset at which 50% of choughs had arrived was significantly positively correlated with day length (Figure 3.8.6) as was the time before sunset at which 50% of choughs had settled in the roost, (Figure 3.8.7). Choughs arrived earlier relative to sunset as day length increased and also settled earlier relative to sunset with increased day length.

Covariance analysis showed that the slopes of the regression lines of arrival and settling times before sunset relative to day length (Figures 3.8.6 and 3.8.7), were significantly different ($F_{1,423} = 25.53$ $p < 0.001$) meaning that the time between arriving and settling was not constant but was dependent on day length.

There was less variation in light intensity at which the choughs settled on the

cliff than in the light intensity at which they arrived, regardless of day length. There was greater variation in time before sunset at which choughs settled than in the time before sunset at which they arrived (Table 3.8.4).

Table 3.8.1 Mean ± s.e. monthly light intensity when 50% of roosting choughs had arrived and when 50% had settled in the communal roost (Roost 1). Light intensity is an arbitrary scale.

	MEAN MONTHLY LIGHT INTENSITY					
	50% ARRIVED			50% SETTLED		
MONTH	mean	s.e.	(N)	mean	s.e.	(N)
JAN.	8.4	0.1	(16)	7.2	0.2	(16)
FEB.	9.7	0.2	(24)	8.0	0.1	(24)
MAR.	10.3	0.1	(21)	7.9	0.1	(22)
APR.	10.6	0.4	(8)	8.0	0.2	(8)
MAY	11.2	0.2	(23)	8.4	0.1	(23)
JUN.	11.7	0.2	(20)	8.4	0.1	(20)
JUL.	11.3	0.2	(34)	8.3	0.1	(34)
AUG.	11.3	0.3	(18)	8.4	0.1	(19)
SEP.	10.4	0.3	(16)	8.2	0.1	(16)
NOV.	9.6	0.1	(5)	7.6	0.1	(5)
DEC.	9.7	0.1	(5)	7.7	0.3	(5)

TABLE 3.8.2 Mean ± s.e. monthly difference in light intensity and time before sunset between when 50% of roosting choughs had arrived and 50% had settled in the communal roost (Roost 1). Light intensity is an arbitrary scale.

	MEAN MONTHLY DIFFERENCE					
	TIME			LIGHT INTENSITY		
MONTH	mean	s.e.	(N)	mean	s.e.	(N)
JAN.	12.8	1.4	(16)	1.2	0.2	(16)
FEB.	13.5	0.9	(27)	1.7	0.1	(24)
MAR.	15.8	0.8	(25)	2.4	0.2	(21)
APR.	14.4	1.3	(9)	2.7	0.4	(8)
MAY	20.6	1.2	(24)	2.8	0.2	(23)
JUN.	27.4	1.3	(25)	3.3	0.2	(20)
JUL.	30.3	1.6	(38)	1.6	0.2	(34)
AUG.	22.9	1.9	(22)	3.0	0.2	(18)
SEP.	13.7	1.0	(16)	2.2	0.1	(16)
NOV.	12.5	1.1	(6)	2.0	0.1	(5)
DEC.	10.0	1.6	(5)	2.1	0.2	(5)

Table 3.8.3 Mean ± s.e. monthly time before sunset (minutes) when 50% of roosting choughs had arrived and 50% had settled in the communal roost (Roost 1).

	MEAN MONTHLY ARRIVAL TIME BEFORE SUNSET					
	50% ARRIVED			50% SETTLED		
	mean	s.e	(N)	mean	s.e.	(N)
JAN.	17.4	1.7	(16)	3.6	1.0	(16)
FEB.	19.1	0.8	(27)	5.6	0.6	(27)
MAR.	21.8	1.1	(26)	6.0	0.8	(25)
APR.	25.8	1.9	(9)	12.4	2.0	(9)
MAY	32.7	1.1	(24)	12.9	1.2	(24)
JUN.	49.2	2.0	(25)	23.0	1.6	(25)
JUL.	51.7	1.4	(38)	21.8	0.9	(38)
AUG.	36.7	2.0	(22)	13.8	1.3	(23)
SEP.	22.9	1.1	(16)	9.2	0.9	(16)
NOV.	14.7	1.1	(6)	3.3	1.3	(7)
DEC.	11.4	1.3	(5)	1.4	0.5	(5)

Table 3.8.4 Coefficient of Variation ± s.e. at 0.01 significance level of light intensity and time before sunset (minutes) when 50% of roosting choughs had arrived and 50% had settled in the communal roost (Roost 1).

	Coefficient of Variation x 100 ± s.e.	
Time before sunset		
50% arrived	47.59 ± 6.57	$p < 0.01$
50% settled	71.49 ± 10.90	
Light intensity		
50% arrived	12.60 ± 1.67	$p < 0.01$
50% settled	8.00 ± 1.06	

FIGURE 3.8.1

Mean ± 1 s.e. monthly light intensity (arbitrary scale) at which 50% of choughs in roosting flock had arrived at the communal roost (Roost 1) and 50% had settled.

Sample sizes can be found in Table 3.8.1

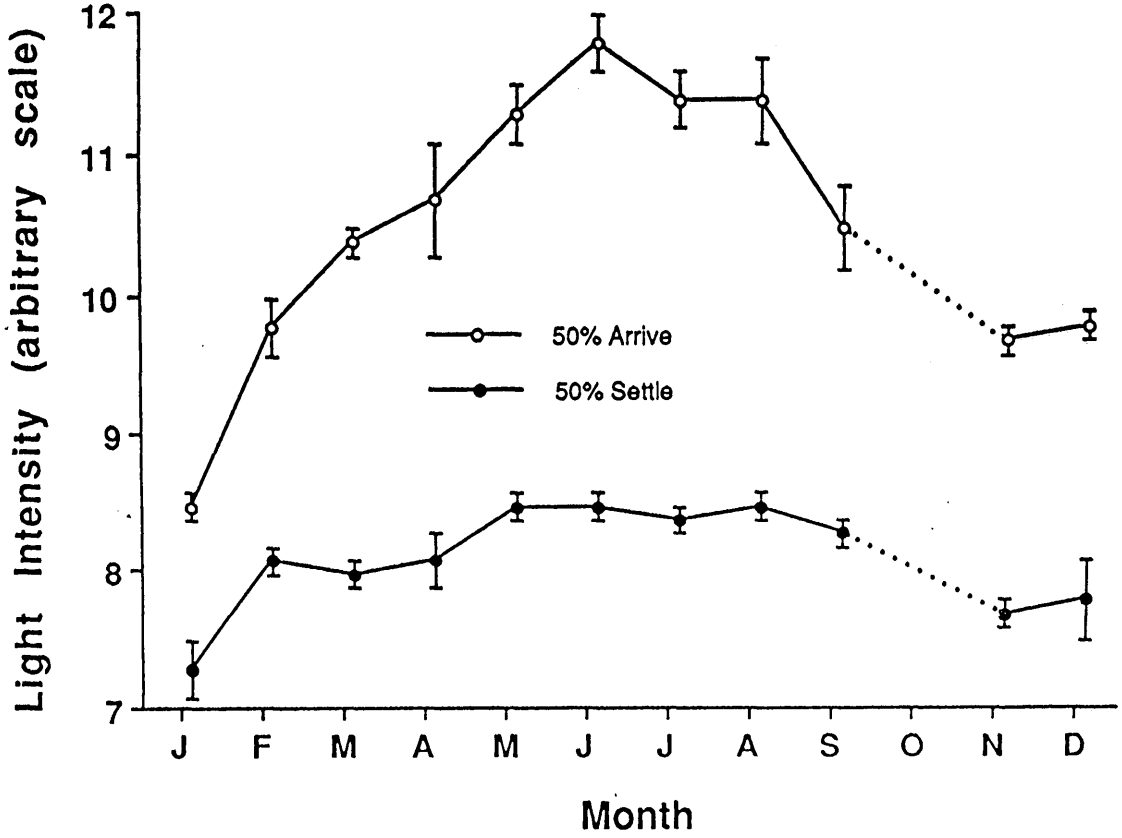

Light Intensity (arbitrary scale)
12
11
10
9
8
7
50% Arrive
50% Settle
J
F
M
A
M
J
J
A
S
O
N
D
Month

FIGURE 3.8.2

Mean $\pm$ 1 s.e. monthly difference in light intensity (arbitrary scale) and time (minutes before sunset) at which 50% of choughs in roosting flock had arrived at the communal roost (Roost 1) and 50% had settled.

Sample sizes can be found in Table 3.8.2

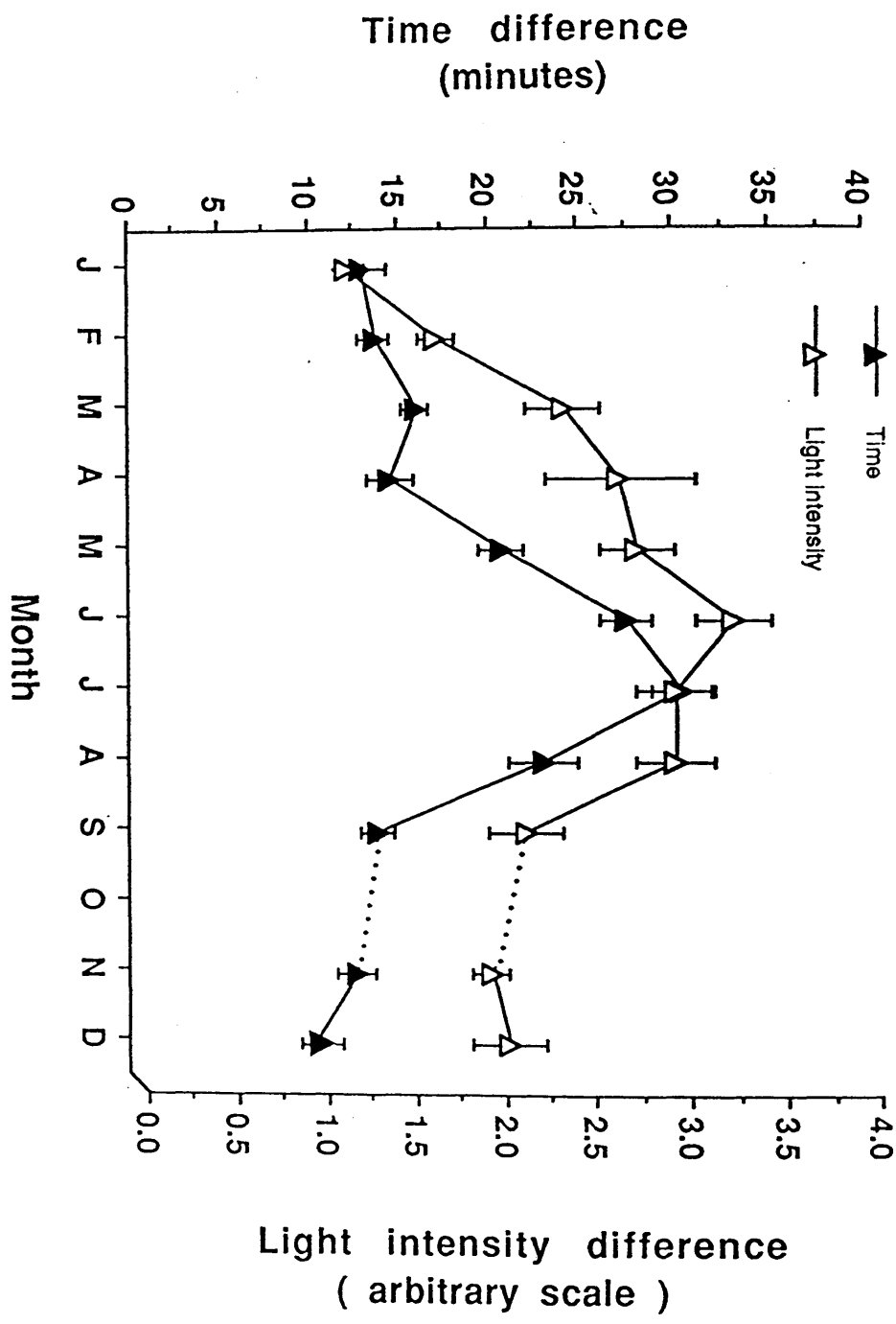

Time difference
(minutes)
0
5
10
15
20
25
30
35
40
Time
Light Intensity
J
F
M
A
M
J
J
A
S
O
N
D
Month
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
Light intensity difference
(arbitrary scale)

FIGURE 3.8.3

Mean ± 1 s.e. monthly time before sunset (minutes) at which 50% of choughs in roosting flock had arrived at the communal roost (Roost 1) and 50% had settled.

Sample sizes can be found in Table 3.8.3

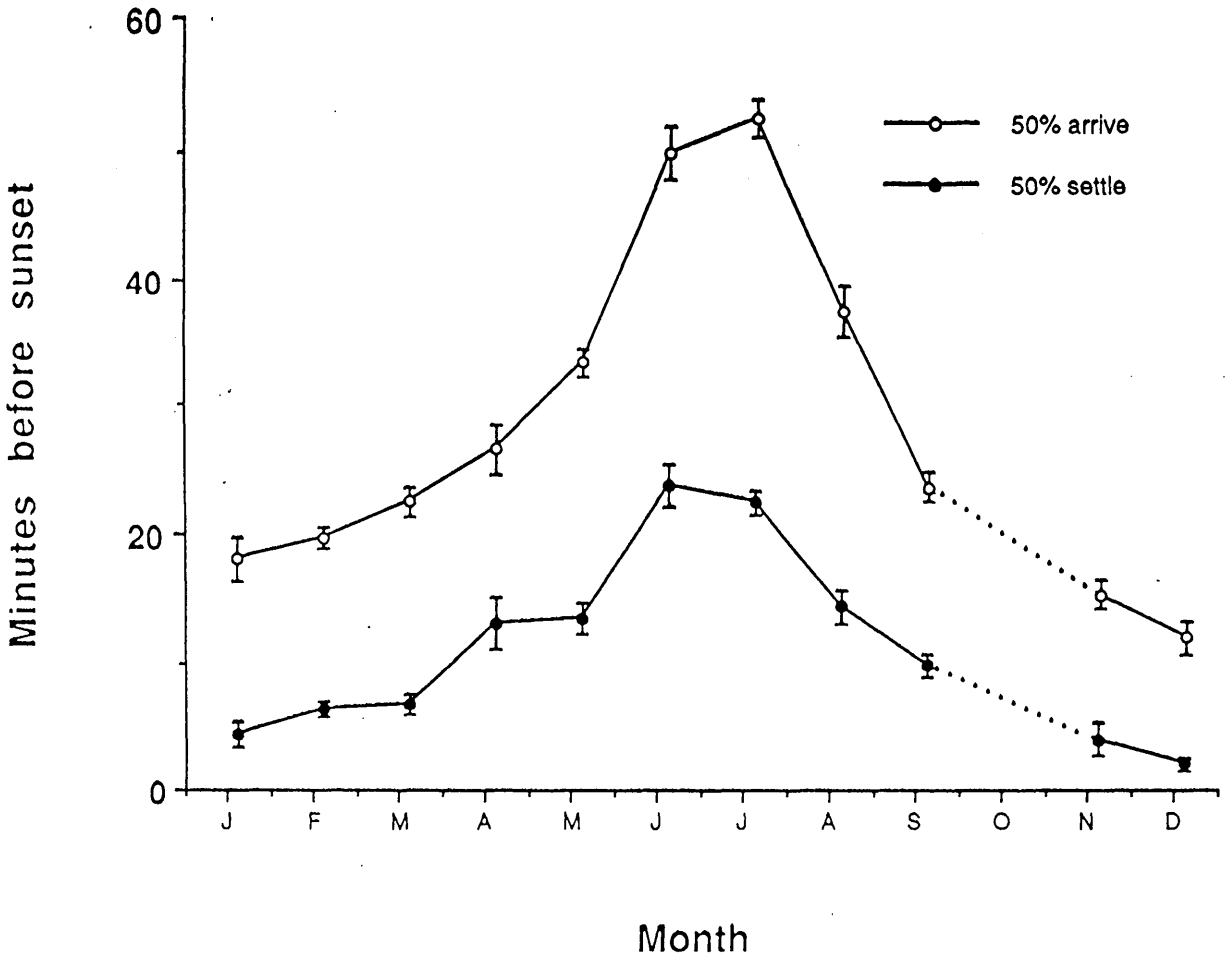

60
40
20
0
Minutes before sunset
50% arrive
50% settle
J
F
M
A
M
J
J
A
S
O
N
D
Month

FIGURE 3.8.4

The association between day length (hours) and the light intensity (arbitrary scale) when 50% of choughs in roosting flock had arrived at the communal roost (Roost 1)

Regression equation $y = 0.27x + 6.90$

$r = 0.70$ $p < 0.001$ 188 d.f.

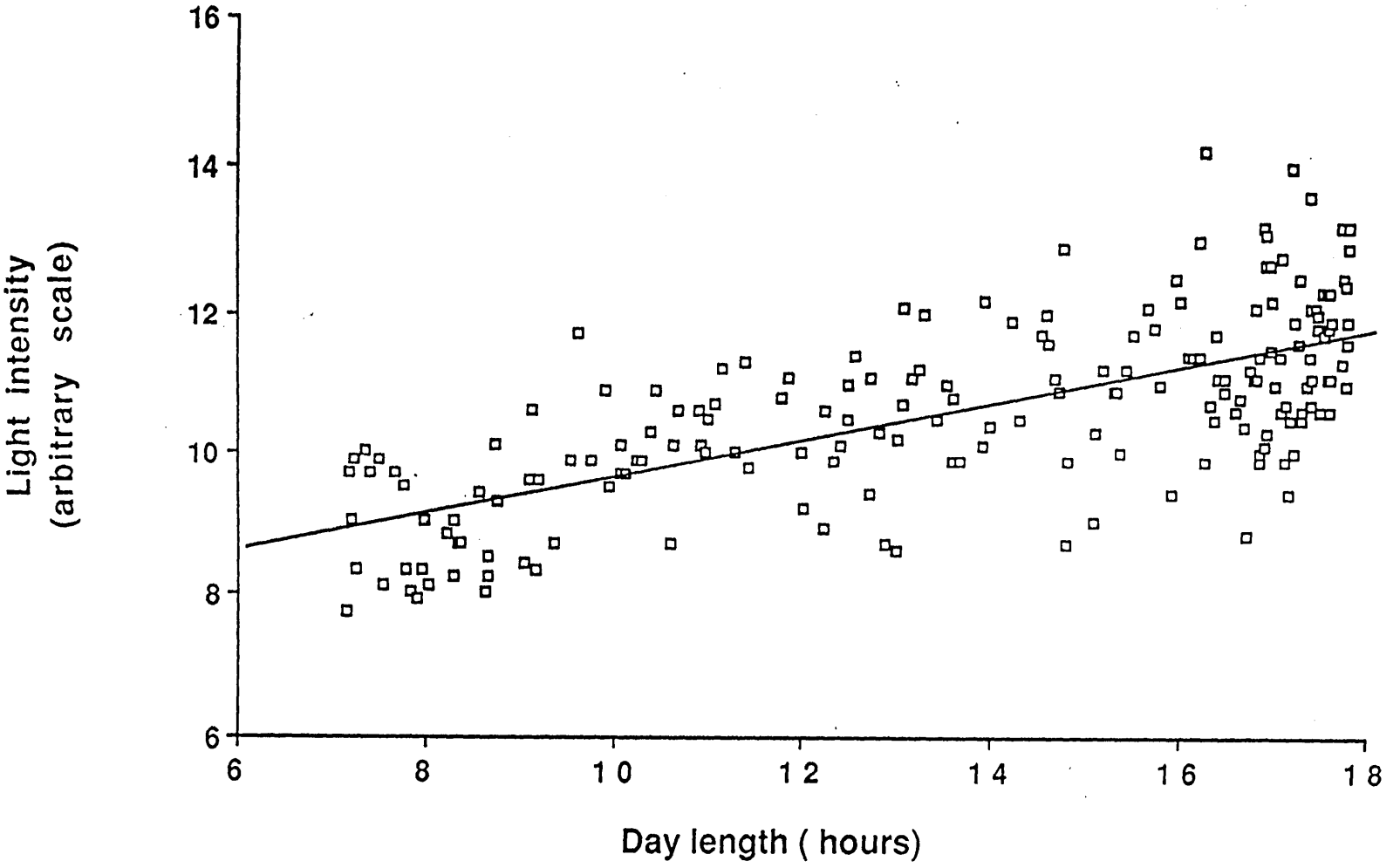

Light intensity
(arbitrary scale)
16
14
12
10
8
6
6
8
10
12
14
16
18
Day length (hours)

FIGURE 3.8.5

The association between day length (hours) and the light intensity (arbitrary scale) when 50% of choughs in roosting flock had settled at the communal roost (Roost 1).

Regression equation $y = 0.08x + 6.97$

$r = 0.44$ $p < 0.001$ 190 d.f.

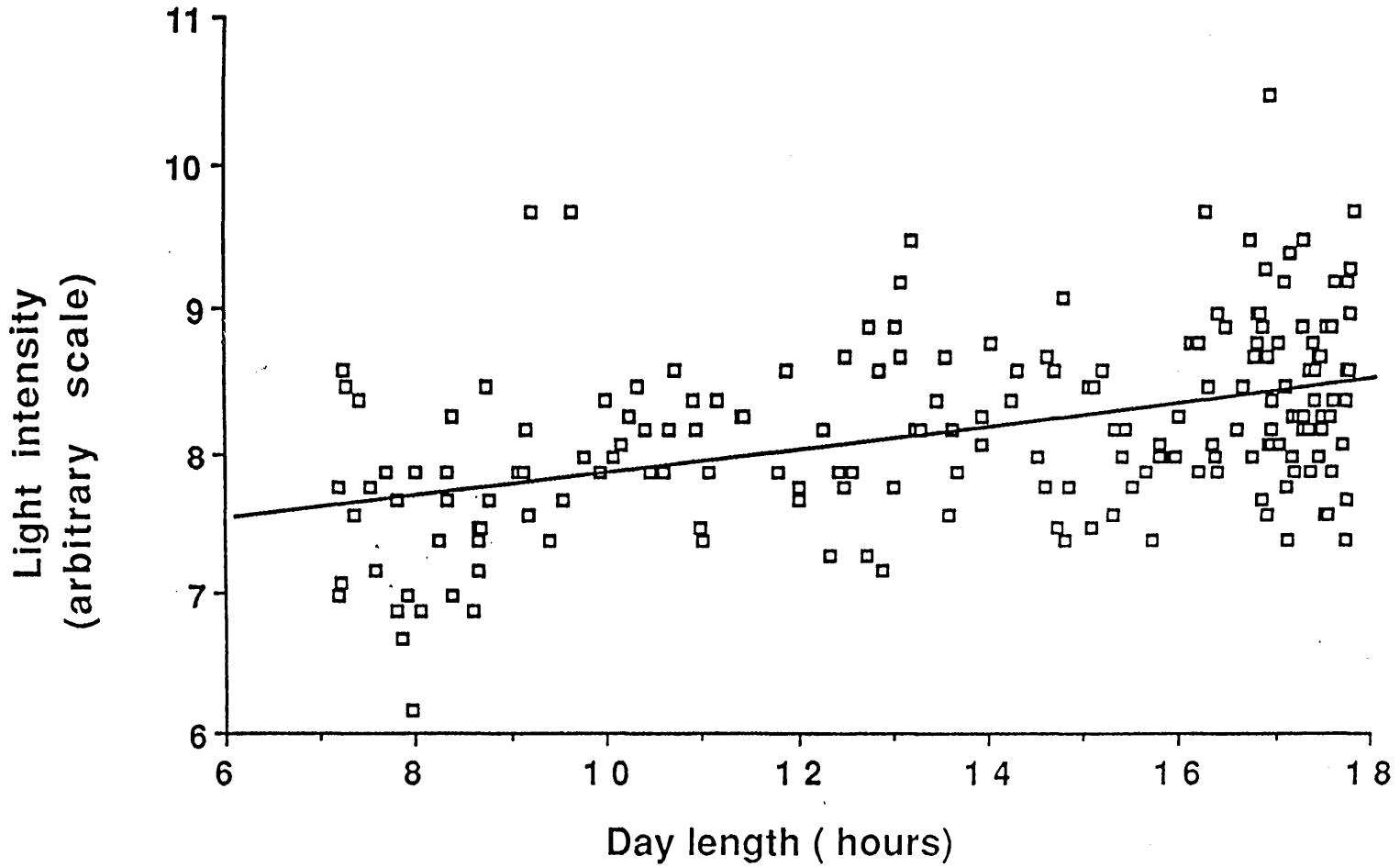

Light intensity
(arbitrary scale)
11
10
9
8
7
6
6
8
10
12
14
16
18
Day length (hours)

FIGURE 3.8.6

The association between day length (hours) and the $\log_{(10)}$ time before sunset (minutes) when 50% of choughs in roosting flock had arrived at the communal roost (Roost 1)

Regression equation $y = 0.049x + 0.80$

$r = 0.83 \quad p < 0.001 \quad 188$ d.f.

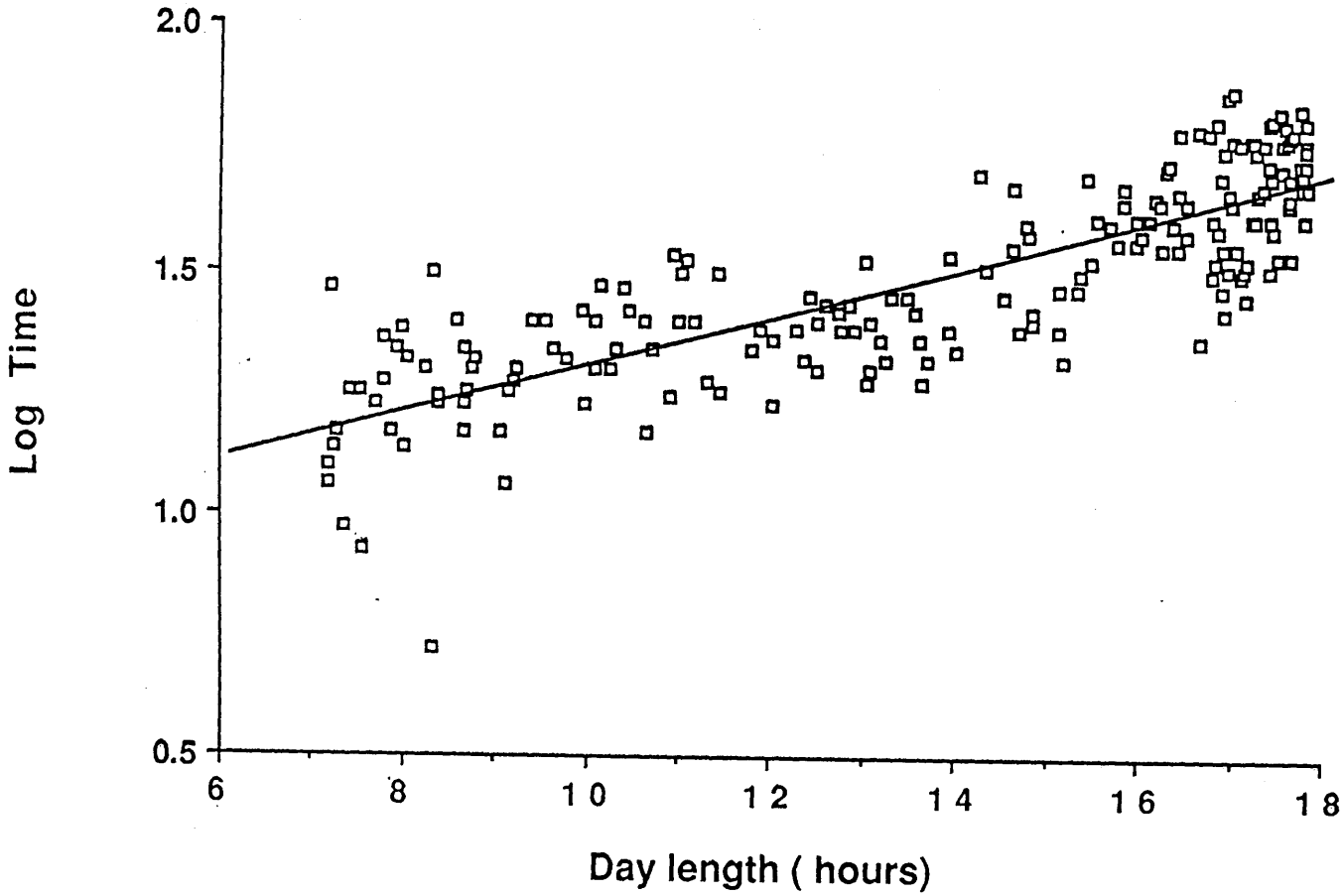
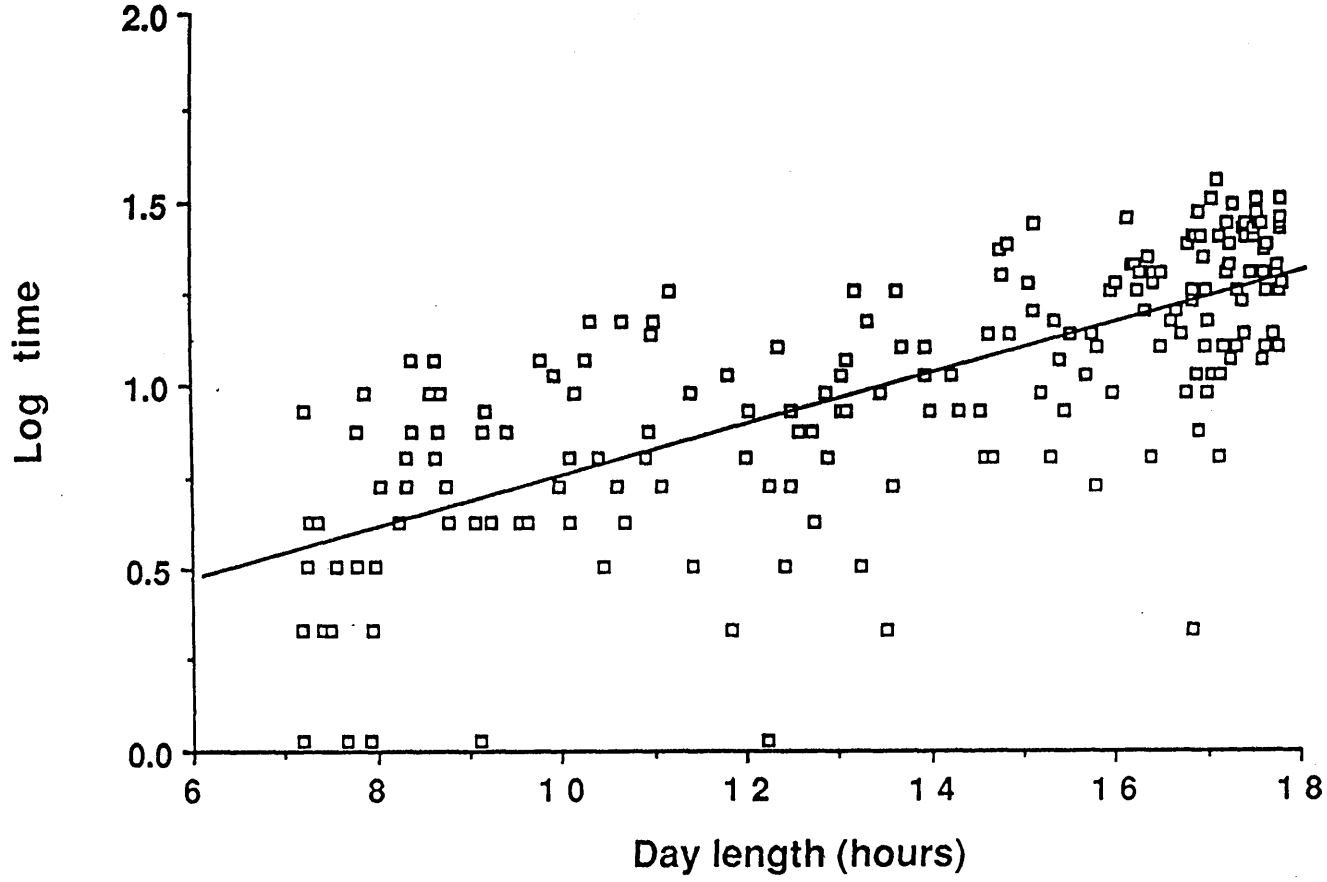

2.0
1.5
1.0
0.5
Log Time
6
8
10
12
14
16
18
Day length (hours)

FIGURE 3.8.7

The association between day length (hours) and the $\log_{(10)}$ time before sunset (minutes) when 50% of choughs in roosting flock had settled at the communal roost (Roost 1)

Regression equation $y = 0.07x + 0.032$

$r = 0.72 \quad p < 0.001 \quad 190$ d.f.


2.0
1.5
1.0
0.5
0.0
Log time
6
8
10
12
14
16
18
Day length (hours)

3.8.4 DISCUSSION.

Choughs arrived at the communal roost earlier in the day and at higher light intensities during the summer months than in winter. During the winter choughs took less time between arriving and settling to roost. Zammuto & Franks (1981) and Michael & Chao (1973) found that chimney swifts (*Chaetura pelagica*) entered their roost at significantly higher light intensities in the warmer summer months than in the colder months. Davis (1955) found that starlings roosted about 30 minutes before sunset in the winter and almost one hour before sunset in the summer. Reebs (1986) found that magpies returned to roost earlier relative to sunset on colder days, longer days and on darker cloudy days. Reebs suggested that early roosting in cold weather may be due to an increased predisposition to inactivity induced by the cold or the possible advantages of shelter in the roost but that these affects may be influenced by the birds levels of hunger. In fact temperature at departure time had no effect in prolonging roosting due to a long night of food deprivation.

Brown (1946), Davis (1955) and Jumber (1956) all found that starlings came to roost earlier in longer day lengths than on short days. Warkentin (1985) found that although merlins left their roost significantly earlier in short day conditions, they entered at the same time relative to sunset regardless of day length. This may be because merlins are visual hunters and cannot feed at the same lower light intensities that sub-soil feeding birds such as the chough may be capable of.

Schnell (1969) for rough-legged hawks (*Buteo lagapus*), Siegfried (1971) for cattle egrets (*Ardeola ibis*), Broom *et al.* (1976) for pied wagtails and Meanley (1965) for mixed species flocks all found that the study species in question roosted earlier during long day lengths than in short day conditions.

As there was less variation in light intensity at settling time than at arrival time and less variation in the time before sunset at arrival time than at settling time suggests that it is light intensity which may trigger the choughs to settle in the roost rather than time relative to sunset. The time before sunset at which the choughs arrived was less variable than the time at which they settled. This sugests that, although their arrival at the roost may depend partly on time before sunset and that circadian rhythms may play a role in triggering choughs to go to the roost, light intensity may decide at what point the birds actually settle to roost.

Kluyver (1957) found that weather conditions had little influence on roosting time in the great tit (*Parus major*) unlike Reebs (1986) who found that cloud cover, temperature and darker days affected roosting time.

Swingland (1976) showed that, for rooks, if a sudden drop in light intensity occurred during the day, they did not go to roost. Harker (1960) demonstrated that there were two light sensitive cycles in the cockroach which interacted and allowed a gradual shift in the timing peak with the change of day length but prevented the animal being affected by changes in light intensity at abnormal times. Achoff (1967) stated that environmental conditions alone do not cause the rhythm of roosting and waking in birds and that this was in fact controlled by a circadian rhythm which could be subtly altered by external conditions.

For the chough, early arrival at the roost in the summer when days are long suggests that they are not constrained in their foraging time during the day and can afford to spend more time at the roost, although not actually roosting, during longer day lengths. Light intensity seems to play a part in the time at which they finally settle to roost however, and showed less variation with day length. Time at the roost during the summer is spent in preening, sun-bathing and social interactions

(pers. obs.). Young, newly fledged choughs are often fed by their parents at the roost when they arrive to roost however, suggesting that the parents have greater constraints on their foraging time than the non-breeding choughs. These newly fledged choughs also spend part of the time involved in exploratory behaviour, older birds often inspecting crevices and holes. Choughs also spend time at the roost involved in communal flights more regularly in the summer than during the winter as has often observed in communally roosting species (Wynne-Edwards 1929, Brown 1946, Davis 1955 and Zahavi 1971b).

4. FLOCKING BEHAVIOUR

4.1 CHAPTER INTRODUCTION.

The flocking behaviour of birds may be dependent on a number of factors. Food type, density and seasonal availability (Crook 1965, Lack 1968, Cody 1971, Thompson *et al.* 1974, Davies 1977), food detection (Ward 1965, Lawrence 1985, Elgar 1989), predation risk (Pulliam 1973, Powell 1974, Siegfried & Underhill 1975, Caraco 1979, Lazarus 1979, Caraco *et al.* 1980, Goldman 1980, Cerri & Fraser 1983, Elgar 1986, Hogstad 1988a), ambient temperature (Caraco 1979, Barnard 1980, Elgar 1986, Hogstad 1988b) may all be factors influencing the numbers, flock composition and feeding behaviour of birds.

The objectives of the following flocking observations were to examine the age composition of flocks of choughs in different areas and seasons, and to determine whether there were differences in the feeding behaviour of choughs related to age, in particular for birds in their first year.

Seasonal variations in flock size and foraging range from communal roosts were investigated. Age related differences in foraging range were examined for one roost (Roost 1) which was in constant use throughout the year and where there were large enough numbers of all age classes to carry out comparisons. Vigilance behaviour and aggressive interactions were studied in flocks of varying size and composition, and while feeding on different food types, to determine some of the factors influencing the feeding behaviour of choughs.

4.2 SURVEYS.

4.2.1 INTRODUCTION.

Set route surveys were carried out in addition to general observations on feeding flocks of choughs to provide a standardised basis from which more detailed and comparative information could be drawn. As choughs moved to other roosts and feeding flocks, set route surveys were carried out to determine the amount of overlap between the foraging distances of choughs using different roosts and thus possibly to define limits within which birds ranged from roosts. If no overlap occurred in foraging distances, then each defined area could be treated as separate observation areas and the behaviour of choughs in these areas compared. Data were collected on foraging distances from roosts and flock size in different seasons. Analyses of survey results would also give an indication for future survey work and censusing on the accuracy of the survey techniques employed here as to the ability to find colour-ringed birds.

4.2.2 METHODS

Set route surveys were carried out and the feeding locations of individually colour-ringed birds recorded. The methods of surveys were as follows; roosts were visited the night before a survey and the colour-ringed birds using the roost were recorded. On the following day, the set route survey was carried out and the roost visited again that night. In this way it is possible to identify the feeding areas of birds known to be using a particular roost. A total of 64 such set route surveys were carried out during the study period.

Individuals found during a survey could be classed as: a) sighted at the roost on both nights, b) sighted at the roost on either of the nights, or c) not sighted at the roost on both of the two nights. The latter does not mean however that birds were

not present as, depending on location of roost or numbers of birds, it was not always possible to identify every single bird at the roost. Choughs seen on only one night or not seen on both nights could have been overlooked as stated above or could have been birds either moving to or from another roost or transient birds in the process of travelling to another area. Therefore since I was not confident of their attachment to a particular roost, birds which were seen during the survey but not seen on both nights at the roost are excluded from analyses of feeding distances from roosts.

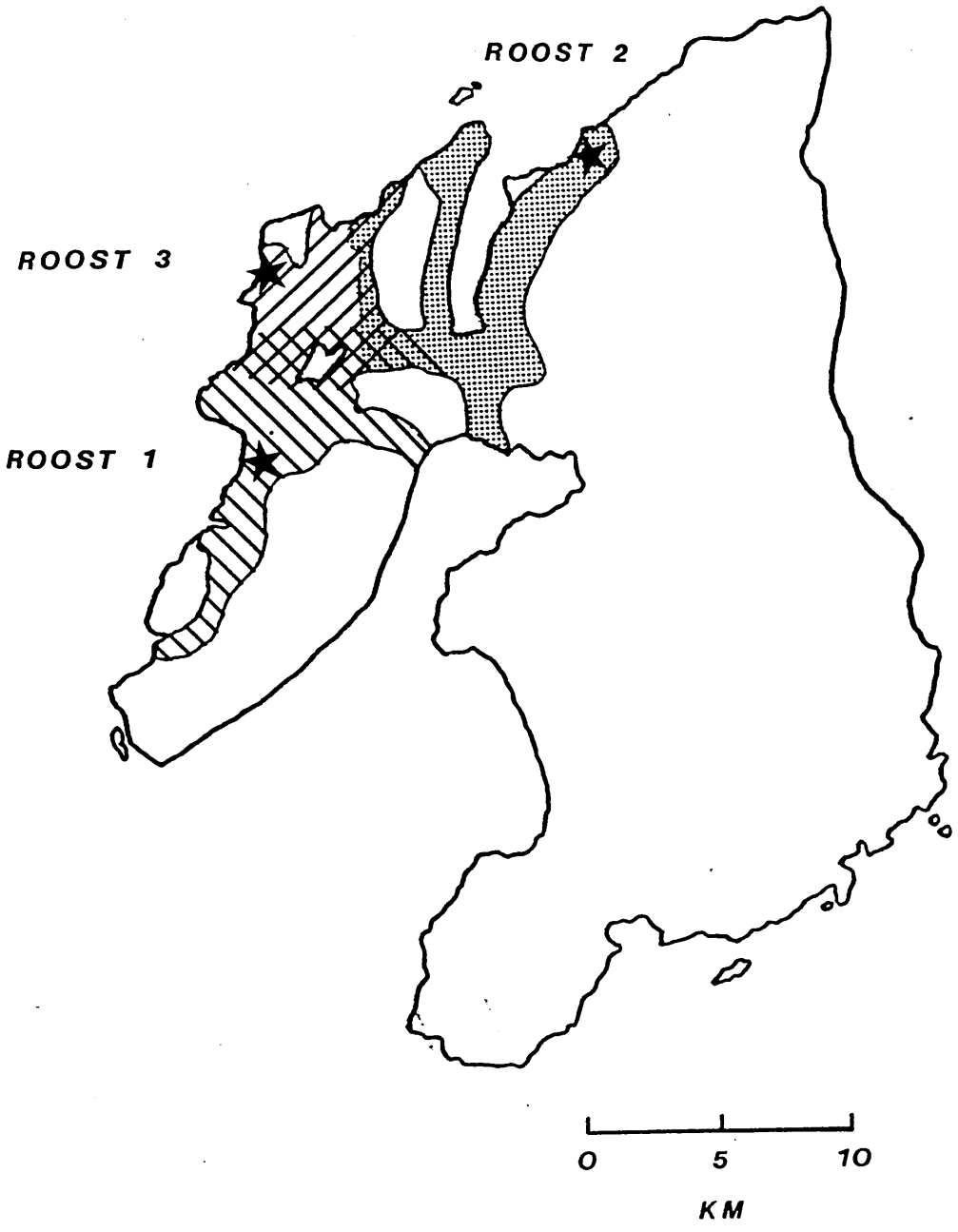
Figure 4.2.1 shows the three survey areas covered and the corresponding roosts visited. The three areas surveyed were chosen on the basis of previous observations of feeding choughs. Surveys also included outlying areas where choughs had seldom or never been seen and covered overlapping sections where adjoining survey areas met.

The numbers of choughs using the three roosts varied between seasons and between years. Roost 1 generally held the largest numbers ranging from 40 to 120. Roosts 2 and 3 were not in continual use throughout the year and numbers varied from 4 to 40 also dependent on season. The largest numbers at Roosts 2 and 3 occurred after the fledging period and during the winter, whereas the largest numbers at Roost 1 occurred during the late spring, fledging period and remaining summer months with lowest numbers in the winter months.

During the surveys the identities of marked birds were recorded along with location, time and flock size. If a particular bird was seen on more than one occasion during a survey, only the first observation of that bird was used in any analyses.

FIGURE 4.2.1

Map of Islay showing the three survey areas and the associated roosts (Roosts 1,2 & 3). Each area was covered during surveys to find colour-ringed choughs which roosted at the associated roost.


ROOST 2
ROOST 3
ROOST 1
0
5
10
KM

Surveys were carried out on a set route by car and on foot. At set points scans were made from suitable vantage points to cover as large an area as possible. The parts of a survey carried out by car were done by driving slowly and stopping at suitable set points and either scanning from the car or walking to a vantage point. Areas away from roads and tracks were walked on a set route, stopping to scan and listen at regular set intervals every 2 to 3 minutes. In some cases, due to the geography of the route, certain areas were covered on the outward and return journey. However. an attempt was made in planning a survey to minimise double coverage and to visit an area only once.

The length of time taken to carry out surveys could not be set as varying weather conditions, location of birds, difficulty of reading colour-rings in different flock sizes, habitat and behaviour of birds affected survey times. During surveys no other data were collected apart from those stated above.

To take into account any temporal differences in the birds' behaviour, surveys were carried out in both the morning and afternoon to get a wider spread of data over the day.

Surveys of an area were carried out only when the corresponding roost was in use. Two of the three roosts (Roosts 2 & 3) were not used by birds throughout the year while Roost 1 was in constant use over the whole year.

Data were split into three 4 month periods to examine seasonal differences in flocking and feeding range. "Spring" was categorised as the period when breeding birds present in the population had left the flocks to either return to a territory or nest site or establish a territory for their first breeding attempt. The time period used was March to the end of June. "Summer" was defined as the period July to the end of October when newly fledged birds first enter the flocks and are often at first

with their parents (July) until the end of October when these first year birds are fully independent. "Winter", (the remaining period), was defined from November to the end of February when daylength is at its shortest and the temperature is also at its yearly minimum. (The start of the "Summer" period could not be set any earlier as it is in July when the newly fledged birds join the flocks. If the period was set from the start of June until November that would result in two cohorts of "first" year birds being present in the analyses i.e. those fledged the previous July and the birds fledging and arriving in the flocks during the present July). Thus the periods reflect not just the prevalent climatic characteristics but also the reproductive cycle of the birds.

Three core areas, defined as being the areas within which 75% of birds from a particular roost were found during the surveys of the three areas were identified. In order to analyse data on flock size within a core area, it was necessary to assign observed flocks to a particular roost. This was done on the basis of flocks being seen in core areas around a particular roost. If a flock was seen outwith the core area but within the distance within which 75% of birds from a roost were found, this flock was also included if the birds were known to have roosted at the corresponding roost that night or a previous night.

There was only one instance of birds from two roosts flocking together (Roost 1 & 3) and this small flock was outwith the 100% boundary lines of the two roosts (defined from surveys). In this case, data from this flock were not included in any analyses.

4.2.3 RESULTS.

Appendix 3 gives details of the numbers, times and months of surveys carried out for the three areas. The proportion of birds which were seen both at the roost (on either or both nights) and during the surveys is fairly constant overall for the three roosts (76% ± 2, 84% ± 2, and 79% ± 3 respectively for Roosts 1, 2 and 3). The 75% boundaries defining the core areas round the each roost are shown in Figure 4.2.2.

It was necessary to check whether there was a relationship between the flock size found on surveys and with proportion of birds. Many small flocks scattered over such a large survey area may have meant that birds were easily overlooked. Alternatively, several large flocks missed or birds missed in large flocks, could have caused the negative relationship between numbers of birds using the roost and proportion found during the surveys.

Figures 4.2.3 - 4.2.5 show the relationship between the numbers of colour-ringed individuals seen at each roost and the proportions of them which were seen during the surveys. For Roost 1 (Figure 4.2.3), there was a significant negative correlation between numbers at the roost and proportion of them which were found on the survey. However, for Roost 2 (Figure 4.2.4), there was a significant positive correlation and for Roost 3 (Figure 4.2.5), there was no significant correlation. For all three roosts there was no significant correlation between proportion of birds found on a survey and the size of the largest flock seen on that day as a proportion of the mean number of birds (ringed and unringed) attending the roost over the two nights (Roost 1 $r = 0.24$, 35 d.f. n.s., Roost 2 $r = 0.23$, 14 d.f. n.s., Roost 3 $r = -0.037$, 9 d.f., n.s.). Therefore, the appearance of choughs in large flocks did not reduce the proportion of choughs found on surveys.

FIGURE 4.2.2

Map of Islay showing the 75% boundary lines from each roost (Roosts 1,2 & 3) within which 75% of colour-ringed choughs from each roost were found during surveys. The "core" area within each 75% boundary line is shown by shading (i.e. core areas 1,2 & 3). Although the core areas of for Roosts 2 and 3 include areas not covered during the surveys, they define the *potential* distances within which 75% of colour-ringed choughs may be found.

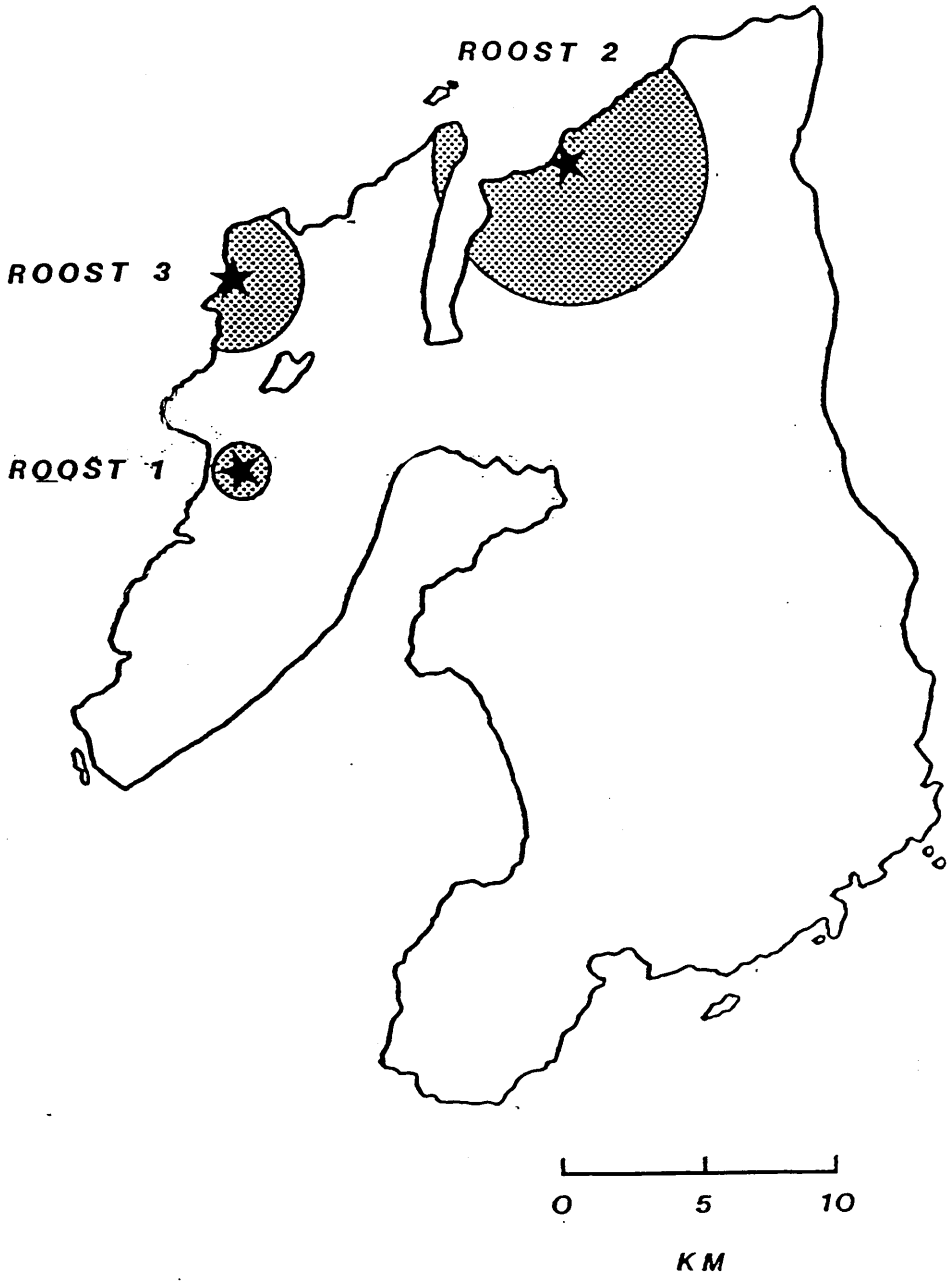

ROOST 2
ROOST 3
ROOST 1
0
5
10
KM

FIGURE 4.2.3

Relationship between the number of colour-ringed choughs at Roost 1 on the night before a survey and the proportion of these colour-ringed choughs which were found the following day during a survey.

regression equation $y = -0.005x + 0.96$

$r = 0.58 \quad p < 0.01 \quad 35$ d.f.

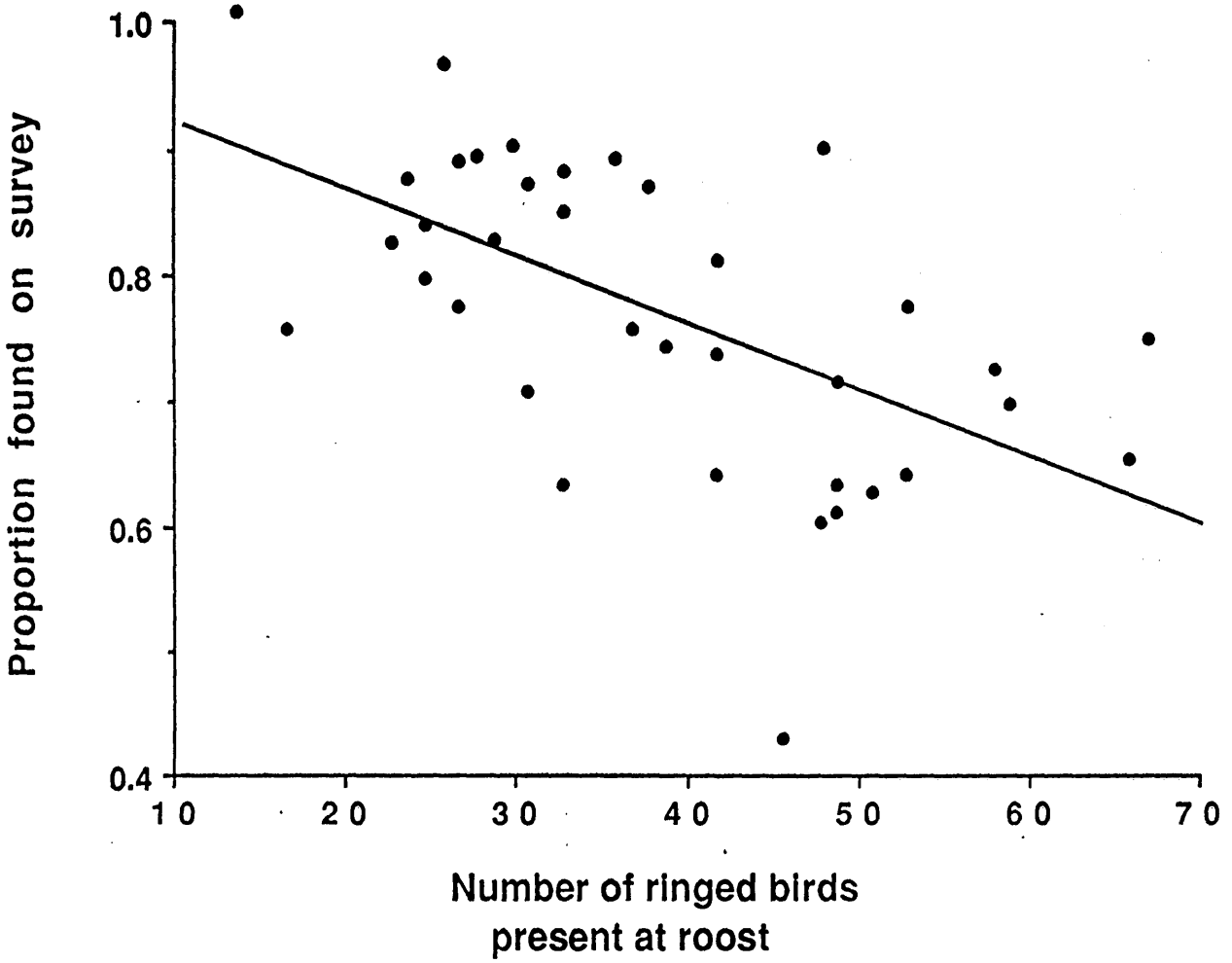

Proportion found on survey
1.0
0.8
0.6
0.4
10
20
30
40
50
60
70
Number of ringed birds
present at roost

FIGURE 4.2.4

Relationship between the number of colour-ringed choughs at Roost 2 on the night before a survey and the proportion of these colour-ringed choughs which were found the following day during a survey.

regression equation $y = 0.02x + 0.47$

$r = 0.57 \quad p < 0.01 \quad 14$ d.f.

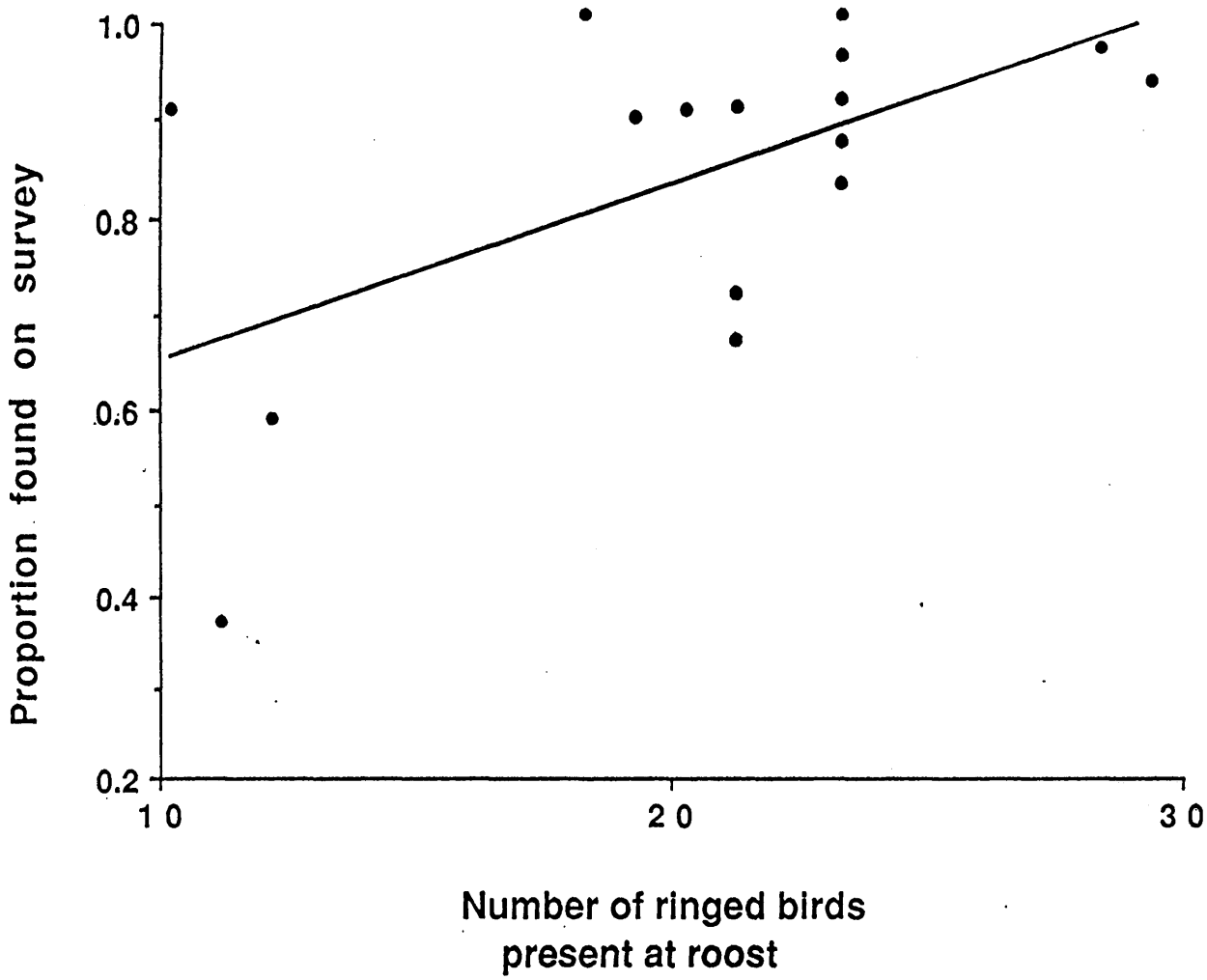
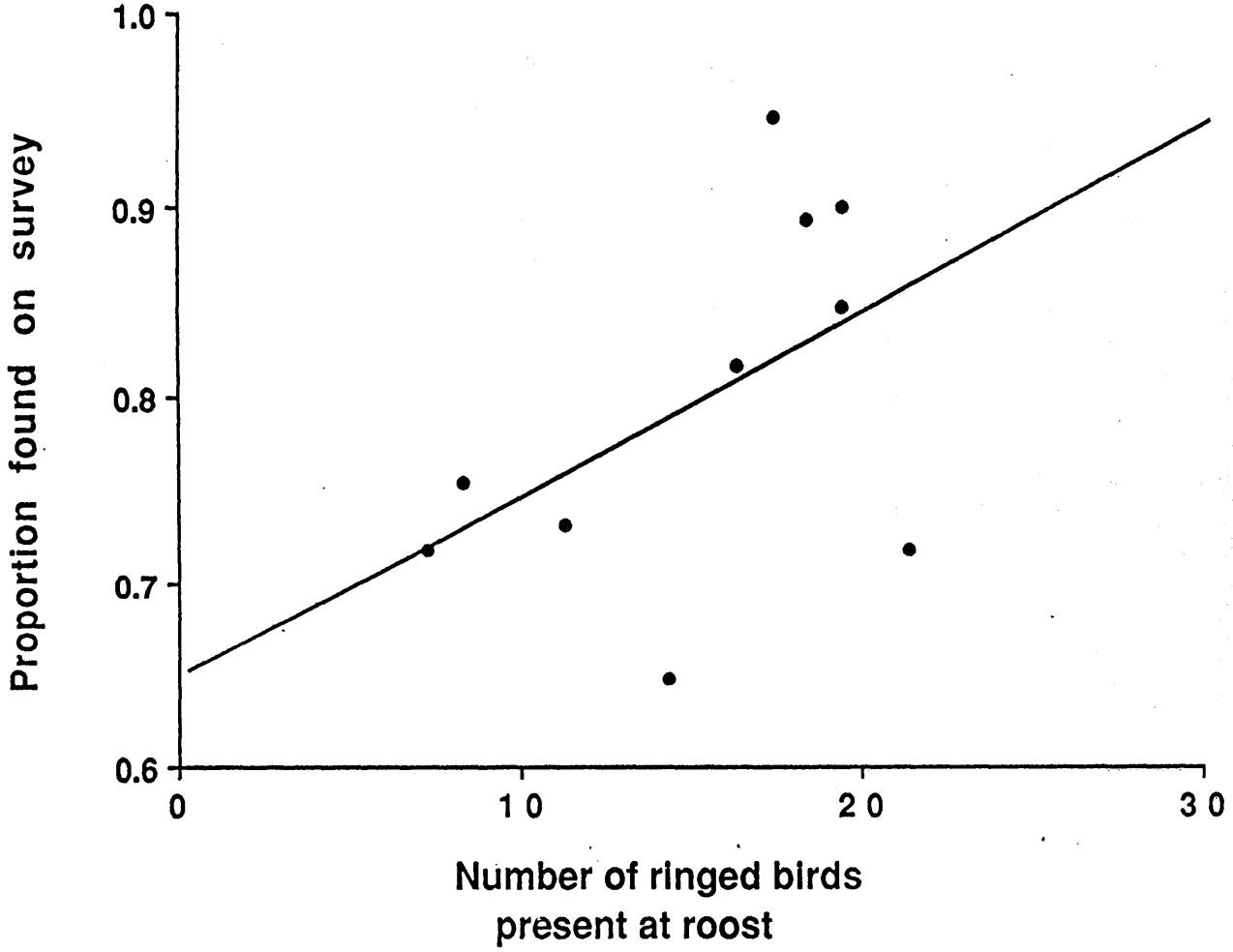

1.0
0.8
0.6
0.4
0.2
Proportion found on survey
10
20
30
Number of ringed birds
present at roost

FIGURE 4.2.5

Relationship between the number of colour-ringed choughs at Roost 3 on the night before a survey and the proportion of these colour-ringed choughs which were found the following day during a survey.

regression equation $y = -0.01x + 0.65$

$r = 0.49$ 9 d.f. n.s.


1.0
0.9
0.8
0.7
0.6
Proportion found on survey
0
10
20
30
Number of ringed birds
present at roost

There was very little overlap in areas used by birds from different roosts. If an area was used by birds from different roosts this usually occurred when one roost was not in use i.e. there was temporal separation in the use of an area by the different groups of birds. There was only one occasion when birds from two roosts were seen feeding together and this was on the extremity of the ranges of Roosts 1 and 3. outwith the 75% boundaries of their respective core areas.

There was no correlation between distance from roost and flock size found on the surveys for any of the three roosts, (Roost 1 r = -0.14, 174 d.f., n.s., Roost 2 r = 0.147, 74 d.f., n.s., Roost 3 r = 0.19, 26 d.f., n.s.).

The results of Table 4.2.1 show that there was a significant difference in the distances travelled by birds to feed depending on which roost they attended. The birds which used Roost 1, (which was the roost in continuous use) travelled the least mean distance to feed. Birds using Roost 2 travelled the furthest mean distance to feed.

There was a significant difference in feeding distance from Roost 1 depending on time of year, (Table 4.2.2). Birds travelled further to feed in the summer and remained closer to the roost in the winter.

There was a significant difference in the foraging range of first year birds in the winter at Roost 1 in comparison with older birds (where there were large enough numbers of older birds to carry out a comparison), first year birds travelling further to feed compared to older birds. There were no significant differences in foraging range between first year birds and older birds in any other season, (Spring; T=-1.87 274 d.f.n.s., Summer; T=0.11 276 d.f. n.s.). The results are shown in Table 4.2.3.

Table 4.2 1. Mean ± s.e. foraging range (km.) from roost of choughs attending each communal roost during surveys. Also shown are the distances in which 50% and 75% were found.

ROOST	MEAN ± s.e. DISTANCE (km.) FROM ROOST	50%	75%	N
1	1.6 0.03	1.5	2.0	708
2	4.2 0.09	4.4	5.0	258
3	2.5 0.04	2.2	2.5	119

One way ANOVA of mean foraging range of choughs at the three roosts $F_{2,1082} = 721.9$ $p < 0.01$

Table 4.2.2. Median foraging range of feeding choughs from Roost 1 for three seasons; Spring, Summer, & Winter.

SEASON	MEDIAN DISTANCE (km.)	N
Spring	1.4	276
Summer	1.5	278
Winter	1.2	154

Kruskal-Wallis ANOVA Test statistic = 7.21
(2 d.f., n=708) $p < 0.05$

Table 4.2.3. Mean ± s.e foraging range (km.) of choughs from Roost 1 at different ages and in different seasons. Sample sizes are shown in brackets. Data are for colour-ringed choughs seen on both nights at the communal roost.

	SEASON								
	SPRING			SUMMER			WINTER		
AGE	mean	s.e.		mean	s.e.		mean	s.e.	
1st	1.5	0.09	(83)	1.5	0.12	(49)	1.9	0.13	(23)
2nd	1.4	0.03	(116)	2.0	0.05	(77)	1.4	0.08	(41)
3rd	1.4	0.03	(59)	1.5	0.10	(92)	1.4	0.06	(67)
4th/5th	1.2	0.12	(18)	1.5	0.02	(60)	1.1	0.07	(23)

T - test on 1st years vs. all older choughs combined during Winter (no significant difference in variance $F_{22,130} = 1.10$ n.s.) T = -2.98 152 d.f.p < 0.005. No significant difference in foraging distances between 1st years and older choughs in Spring and Summer.

FIGURE 4.2.6a

The percentage of flocks of choughs found on surveys which were in differing size categories in "Spring" (March - June). Data are for core area 1 (i.e. choughs using Roost 1).

Sample size - 67 flocks

FIGURE 4.2.6b

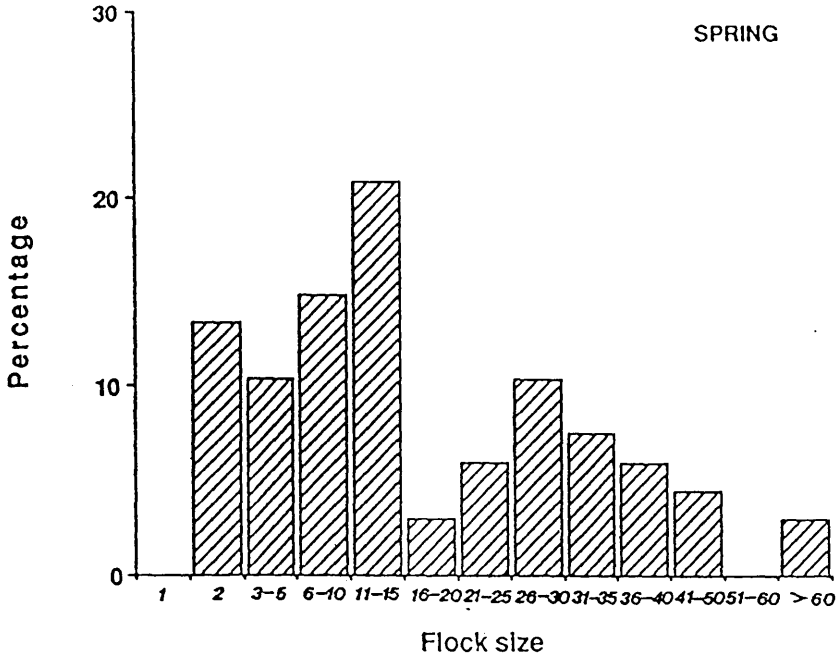
The percentage of flocks of choughs found on surveys which were in differing size categories in "Summer" (July - October). Data are for core area 1 (i.e. choughs using Roost 1).

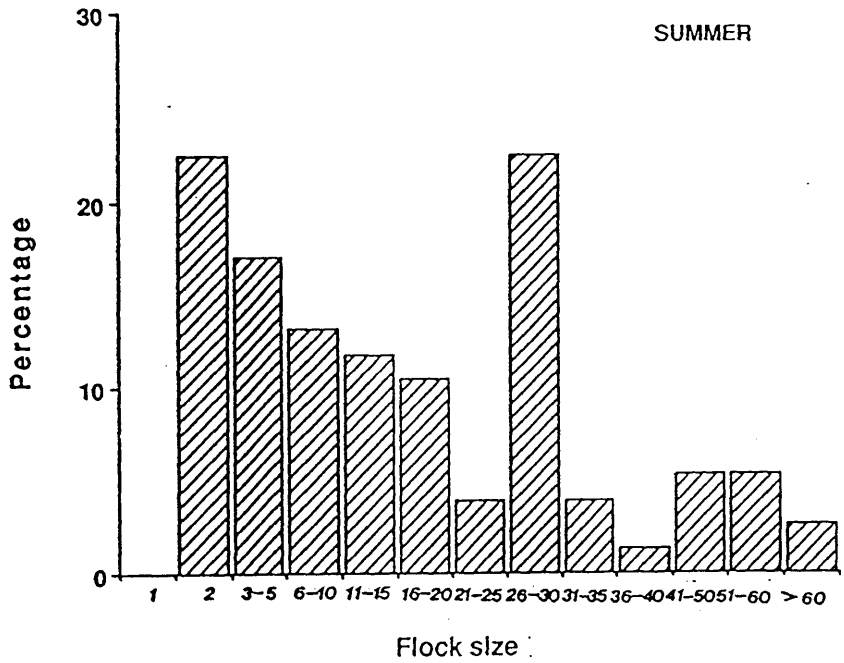
Sample size - 76 flocks

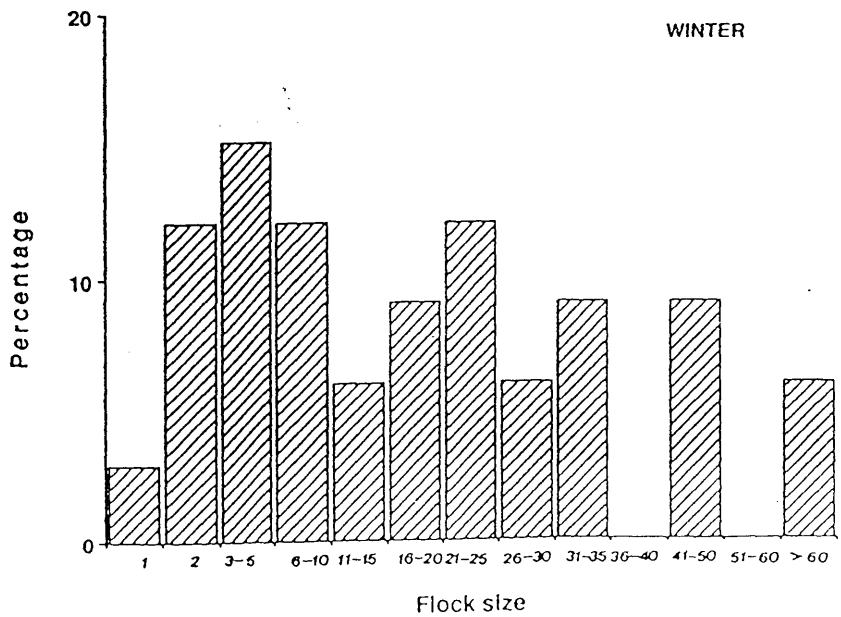
FIGURE 4.2.6c

The percentage of flocks of choughs found on surveys which were in differing size categories in "Winter" (November - February). Data are for core area 1 (i.e. choughs using Roost 1).

Sample size - 33 flocks


SPRING
Percentage
30
20
10
0
1
2
3–5
6–10
11–15
16–20
21–25
26–30
31–35
36–40
41–50
51–60
> 60
Flock size


SUMMER
Percentage
30
20
10
0
1
2
3–5
6–10
11–15
16–20
21–25
26–30
31–35
36–40
41–50
51–60
> 60
Flock size


WINTER
Percentage
20
10
0
1
2
3–5
6–10
11–15
16–20
21–25
26–30
31–35
36–40
41–50
51–60
> 60
Flock size

Figures 4.2.6a-c show the distribution of flock sizes in the core area around Roost 1 during the three seasons. There was no significant difference between the seasons in the distribution of observations of differing flock sizes. There was a trend however for an increase in the proportion of flocks of two in the spring and summer compared to the winter, with flocks of two being the most prevalent flock size during the summer. The largest proportion of flock sizes during the winter and spring was between 21 and 40.

4.2.4 DISCUSSION.

For Roost 1, the proportion of birds found on the surveys decreased as numbers at the roost increased suggests that survey coverage for this area was not as complete as it should have been. However, at the lowest, 42.2% of birds were still found. The method of survey in this area may have been open to more error than in the other areas. Several large areas became completely hidden while other parts were being surveyed. This meant that movements of birds may not have been seen. A journey between one part of the survey area and another to get round some inland cliffs was the main reason for this as it meant leaving the survey area completely. In the other two survey areas, round Roosts 2 and 3, it was possible to keep much of the rest of the survey area in view.

The significant correlation between ringed birds at roost and the proportion of them which were found for the surveys for Roost 2 are difficult to interpret. It may be that there were fewer potential feeding sites for birds at this roost and as numbers using the roost increased they flocked together making them easier to locate. Also, the maximum numbers of birds using Roost 2 were fewer than at Roost 1 and in general may have made it easier to find a higher proportion of birds in a smaller area. The slight (but not significant) positive trend in the same

correlation for Roost 3 may also be due to the same effects suggested above for Roost 2. In none of the three survey areas was the ability to find birds related to the existence of larger flocks.

There is no overlap in the 75% core areas of the three roosts. Birds which are using one particular roost do not feed within the 75% core area of another roost. Although some individuals may forage further away than the 100% boundary they were not seen in the company of birds using another roost except on the one occasion. Choughs do not defend these core areas against birds from other roosts and birds are able to move freely from one core area to another, although once there, they tend to stay.

There was practically no movement of birds back and forth between roosts on a nightly basis. One bird was seen to roost at Roost 3 for several months, then join birds at Roost 1 and feed in Roost 1 core area for two nights then return to Roost 3 and remain there. It is difficult to pick up movements within a night however as two roosts cannot be observed in the space of one night.

Loman (1985) found that the home ranges of non-breeding crows overlapped widely and that changes of roosting place were common. He also noted that juvenile crows changed area in the course of the winter more so than older birds.

Non-breeding birds move freely within the feeding ranges of breeding choughs although non-breeders which are paired and enter the breeders territories are more likely to be involved in aggressive interactions than larger flocks of non-breeders. These non-breeding pairs may pose more of a threat to breeding birds as they may be prospecting for nest sites. Charles (1972) found that non-breeding crows used marginal habitats outwith the territories of breeders. This is not true for choughs or for magpies (Birkhead *et al.* 1986, Eden 1989). Bohmer 1976 (in Loman 1985) found

that territorial crows probably had no influence on the distribution of flocks.

Breeding choughs regularly join non-breeding flocks to feed with little or no aggressive behaviour. This has been noted by many authors, (Williamson 1959, Holyoak 1972, Coombs 1978, Warnes 1983a, Roberts 1985). Also, flocks often feed within breeders territories. This suggests that movements of choughs to feeding sites is not influenced by any territorial behaviour of breeding birds. As an additional note to this, mass displays comprising in one case 16 birds were seen (although infrequently), and usually when flocks of non-breeders were feeding with breeding birds within the breeders territories. This usually occurred in the spring when non-breeders would be moving from the non-breeding flocks to find a nest site. These mass displays have been noted in magpies (Birkhead & Clarkson 1985) and crows (Charles 1972) and been related to territory acquisition where breeding habitat is saturated.

Choughs taking part in these mass displays are usually non-breeding but paired birds. These displays involve bowing, wing flicking and usually a great deal of with birds often walking slowly together in the same direction. This has only been noted by Holyoak (1972) although the explanation he gave was that these displays were due to attacks on displaying birds with other birds joining in. These mass displays also form round fighting birds in areas away from breeding territories. However, they differ from the mass displays on territories as territorial mass displays often involve little physical aggression. This also suggests that breeding birds accept non-breeders within their territories and that any territorial defence or display by breeders is reserved for potential competitors for their nest site.

A function of flocking by non-breeders is that it may allow them undisturbed access to breeders' territories without incurring any territorial aggression by the resident pair. It may be useless for breeding birds to attempt to chase off large numbers of non-breeders. Robertson *et al.* 1976 suggested that schooling by some

species of tropical fish may be a method of avoiding the territorial aggression of resident fish thus allowing the school members free access to feeding sites and shelter.

For Roost 1, which was in use all year, it was found that there was a significant difference in feeding range depending on time of year. The feeding range was smallest in the "winter" and largest in the "summer". Macdonald & Whelan (1985) found that for rooks, foraging range increased in late summer and late winter when food availability was either generally low or locally distributed. Patterson *et al.* (1971) found that the winter feeding range of rooks in northeast Scotland was quite restricted, being smaller than in the spring. Changes in food availability accounted for these differences. During long day length, birds ranged further from the roost. Obviously, feeding distance will be closely related to the appearance of suitable food sources around the roost.

For choughs using Roost 1, suitable feeding areas are available close to the roost at a time of year when daylength is at its shortest and birds arrive at the roost later relative to sunset than in the summer months, (see section 3.8.3). However, when the feeding range of first year birds is compared to that of older birds, first year birds in the winter forage significantly further away from the roost. This is occurring at a time when day length is at its shortest. It may be that these younger subordinate birds are being pushed out of feeding sites close to the roost. Fourth and fifth year birds are foraging closer to the roost than younger birds.

Foraging range is at its greatest during the summer months. Birds can travel further in search of food without being constrained by day length. Seasonal changes in food availability may be partially responsible as birds home in on food sources as they become accessible. Another possible factor in the apparent increase of

feeding range in the summer is the movement of family groups which had bred within several kilometres of the communal roost returning to, or close to, their breeding site during the day, before returning to the communal roost in the evening (pers obs.).

The other two roosts in this study were not used continuously throughout the year and when used, generally contained younger, subordinate birds, (see section 4.3.3). The separate roosting and feeding of juvenile rooks has been noted by Coombs (1961) and Dunnet *et al.* 1969, and for starlings (Henty 1989). It may be that Roost 1 offers the best roost site for year round use in its proximity to food sources especially in the winter, although first years in the winter travelled further to feed (birds also travelled further to feed at the other roosts [Roosts 2 & 3] which contained the highest proportions of young birds). Food availability may be at its lowest during the winter months and this is the time of highest mortality of young choughs (Bullock *et al.* 1983a, Roberts 1985, Bignal *et al.* 1987). This may be a period when choughs are most stressed and this stress may be greater for subordinate first year choughs which also travel furthest to feed during short days. These first year choughs travellled nearly twice as far as 4th/5th years, (Table 4.2.3). Overall, choughs did not range far from their roost sites. Warnes (1983a) found a maximum distance of 5 km. Bullock found a maximum feeding range of 8.2 km. However, the results from this study were taken on surveys only and did not include casual observations. If these were taken into account, the range would be greater. The maximum distance choughs were known to travel from Roost 1 and only for birds which were seen on both nights at the roost was 8.0 km.

One strategy to take advantage of changes in food availability is to move to other roosts around which food availability may be temporarily high. Warnes (1983a)

found that chough roosts on Islay were not in use all year and numbers using these roosts varied throughout the year. In this study this seemed to occur at Roosts 2 and 3 which were not in use over the whole year.

There was a core of older birds at Roost 1 during the winter, the numbers of which did not drop to the same extent as first and second year birds. Older dominant birds can remain at Roost 1 during the winter and take advantage of available food sources and maybe push younger subordinate choughs to other areas. Loman (1985) suggested that movement by juvenile crows to other areas was the result of their lower dominance rank and pressure of food competition especially in the winter.

There may be an advantage in remaining in a feeding area and at one roost as familiarity with the area may make food finding more efficient. Knowledge about suitable feeding sites which may change seasonally may allow birds to spend less time sampling the feeding area and thus allowing more time to be spent feeding. Familiarity with a roost may also allow choughs to find and maintain the best roost sites and to maintain their position in the social hierarchy.

Holyoak (1972) stated that on the Isle of Man, most non-breeding choughs are paired during the late spring and summer. This fits with the findings on chough flock size in this study during surveys. Although paired non- breeders were usually found within larger flocks, they often fed separately from other non-breeders. This accounts for the large peak in sightings of flocks of two during the summer. Lovari (1976) found that chough flock sizes in the Abruzzo National Park in Italy were at their lowest during the winter which does not correspond to the findings of this study. Possible differences in diet and climate may account for these variations. Large flocks in this study were often found on stubble fields in the autumn and winter which may account for the large proportion of flock sizes of 21 to 40, (Figure 4.2.6c). Warnes (1983a) found that the most common flock size of choughs

on Islay was 2 throughout the year in her "North Rhinns" area which corresponds to the core area in which these observations were based. Warnes also found a large proportion of single choughs (20%) during the winter which is also unlike the findings here. She further found that only 10% of flocks were greater than 9. It is difficult to account for these differences in distribution of flock sizes between this study and Warnes' study in 1980/1981. An increase in the numbers of choughs may partly account for a general increase in flock size. The largest roosting flock at Roost 1 during Warnes' study was 56 which is considerably smaller than numbers generally using this roost during this study. As the numbers of non-breeders increase, birds may then have to flock in larger numbers if food availability has remained constant between 1980/1981 and at present.

In summary:-

Between 76 and 84% of choughs which used the three study roosts were foung during surveys.

There was no correlation between the proportion of choughs found on a survey and the size of the largest flock seen that day.

There was no correlation between distance from roost and flocksize.

There was a significant difference in the foraging range of choughs from different roosts.

The foraging range of choughs at Roost 1 was greatest in the summer and smallest in the winter.

First year choughs foraged significantly further from Roost 1 than older choughs in the winter although there was no significant difference during other seasons.

There was no seasonal difference in the frequency distribution of flock sizes.

For each roost, the surrounding core area in which 75% of choughs from that roost were found did not overlap with any other core areas. There was no "territorial defence" of these core areas.

4.3 AGE STRUCTURE OF FEEDING FLOCKS.

4.3.1 INTRODUCTION.

The proportions of different ages of birds in different areas and/or flock sizes has been noted in rooks where Burkitt (1935), Coombs (1960 & 1961) and Dunnet *et al.* (1969) found some evidence that young and old rooks may tend to segregate partially in the autumn and early winter with young birds often using an area different from that used by most of the local adults. Henty (1989) noted that juvenile starlings often assemble into flocks which are practically entirely composed of other juveniles. Dunnet *et al.* (1969) also found that the proportion of young rooks in flocks decreased with increased flock size. The object of the following work was to examine the proportion of birds of different age classes in flocks of different sizes and in different core areas.

4.3.2 METHODS.

The age composition of flocks was estimated using sightings of colour-ringed birds. To examine the feeding flock structure of choughs using different roosts, it was necessary to assign observed flocks to a particular roost. This was done on the basis of the flocks being seen in core areas around a particular roost, (core areas were defined as areas within which 75% of birds from a particular roost were found on the basis of the surveys described earlier). Thus, flocks seen within each core area were assigned to the appropriate roost. Birds which were seen outwith the 75% level or on the boundary between two core areas were assigned to a core area and roost only if they were known from colour-ring sightings to have attended the appropriate roost either the night before or the night of the observation. Otherwise these flocks were excluded from the analyses.

Paired choughs were not included in the analysis if they were observed as a flock of two on their breeding territory or territory they held although not breeding. These birds were included however while on a territory but in flocks greater than two, i.e. associating with other birds. Non-breeding choughs often feed in the breeding territories of breeders as has been observed by Holyoak (1972). Including pairs on territories where one or both birds are colour-ringed would bias the data on age proportions as these birds form a stable association and cannot be regarded as a non-breeding flock. For example, if there were many sightings of a second year bird paired to a fourth year bird on a territory, this would bias the age proportion results for flocks of two.

Choughs which appeared to be paired but without territories and which fed and roosted with other non- breeders were included in the analysis as it is difficult to define whether they were a stable pair. As the analysis on flock structure was carried out to ascertain whether choughs chose to flock with certain other birds, one could argue that non-breeding (but paired birds) which roost and usually feed with other non-breeders have more potential to choose whether to join other non-breeders. In contrast, territorial choughs with or without young may have conflicting interests in whether to join flocks or maintain their territories and thus exclude non-breeders or other potential breeders competing for the same nest site.

In the same way that paired birds on territories were excluded from the analyses, so also were family groups composed of newly fledged birds with their parents while feeding together on the breeding territory.

Data were combined for different cohorts at the same age. From personal observation there was nothing to suggest that certain ages of birds were more observable than others. Dunnet *et al.* (1969) suggested that one reason for finding a higher proportion of young rooks in small flocks was that younger birds could be

less observant and fly off less readily than older birds. In their study they were dealing with much larger flocks in general and may not have observed as readily as was possible in this study if birds had left the flocks. Thus, data on flocks in which not all choughs were checked for colour-rings, (but at least one third of the flock or over was checked), were also included since the overall flock composition could be estimated from the sample. As incomplete checks for colour-ringed birds usually occurred in large flocks, a sample would be less inaccurate than a sample from a small flock.

Data from fourth and fifth year birds were combined due to small sample sizes. Data on age proportions were arcsine transformed before statistical analysis and the proportions of 1st, 2nd, 3rd, and 4th/5th year old birds were examined in relation to flock size.

4.3.3 RESULTS.

As the proportion of one age class changes one would expect this to affect the proportions of the remaining ages present. However, if for example 30% of the population of colour-ringed choughs are first years, then, regardless of the flock size, the null hypothesis is that 30% of all colour-ringed birds in the flock should be first years if they are distributed randomly between flocks. Obviously, the smaller the flock size or number of colour-ringed birds in a flock, the greater the effect on proportions one individual colour-ringed bird would have.

Since 35 correlations are examined, there is an increased chance of a Type 1 error if the 5% probability level is used (2 significant results being present by chance). Therefore only results significant at the 1% level are classed as robust. Also, large

sample sizes mean that one may get statistical but not biological significance since only small amounts of variation may be explained, as shown by the coefficient of determination (r^2).

Table 4.3.1 presents the coefficient of determination along with correlation coefficient, probability value and sample size of age proportion in relation to flock size for four age groups in the three core areas during the three seasons (spring, summer and winter) as defined earlier. The results are also depicted in Figures 4.3.1a-c, 4.3.2a-c and 4.3.3a-c. Data were combined into groups of flock sizes and the means $\pm$ 1 s.e. and sample sizes can be found in Appendix 4.

For first year birds in core area 1 in spring as flock size increased, the proportion of first year birds tended to decrease.

As flock size increased there was a larger proportion of 2nd and 3rd year birds particularly in winter. Older birds (4th/5th year birds) also showed this trend in spring although in summer and winter there was no significant correlation between flock size and proportion of these birds.

In core area 2, there was generally no correlation between the proportion of first year birds and flock size in any season. For 2nd year birds there was a positive, significant correlation between flock size and proportion found but only in spring. For all older age classes (3rd & 4th/5th years) there was no correlation between proportion found and flock size.

In core area 3, first year birds occurred in significantly lower proportions in large flocks in summer and winter. There was a significant positive correlation between increasing flock size and proportion of 2nd year birds in flocks in summer only. There was no correlation for 3rd year birds in spring and summer and also for

4th/5th year birds in summer. However there were no 4th/5th year birds in area 3 in the spring. For both age classes there was a significant positive correlation between flock size and proportion found during the winter.

Table 4.3.1. Correlation between age proportions of colour-ringed choughs and size of feeding flocks within the three core areas used by choughs attending Roosts 1, 2 & 3.

AGE	r	r^2	p	N
		AREA 1 (ROOST 1)	SPRING	
1st	-0.186	0.035	0.01	407
2nd	0.251	0.063	0.01	407
3rd	0.175	0.031	0.01	407
4th/5th	0.173	0.030	0.01	236
		AREA 1 (ROOST 1)	SUMMER	
1st	-0.084	0.007	0.02 (n.s.)	749
2nd	0.303	0.092	0.01	749
3rd	0.073	0.005	0.05 (n.s.)	749
4th/5th	0.020	0.000	n.s.	1103
		AREA 1 (ROOST 1)	WINTER	
1st	-0.137	0.019	0.02 (n.s.)	317
2nd	0.414	0.171	0.01	317
3rd	0.190	0.036	0.01	317
4th/5th	-0.022	0.000	n.s.	256
		AREA 2 (ROOST 2)	SPRING	
1st	-0.001	0.000	n.s.	56
2nd	0.707	0.500	0.01	56
3rd	-0.250	0.062	n.s.	56
4th/5th	0.219	0.048	n.s.	56
		AREA 2 (ROOST 2)	SUMMER	
1st	-0.016	0.000	n.s.	109
2nd	0.166	0.028	n.s.	109
3rd	0.168	0.028	n.s.	109
4th/5th	-0.101	0.001	n.s.	157
		AREA 2 (ROOST 2)	WINTER	
1st	0.131	0.017	0.05 (n.s.)	235
2nd	-0.027	0.001	n.s.	235
3rd	0.048	0.002	n.s.	235
4th/5th	0.034	0.001	n.s.	330

Table 4.3.1 cont. Correlation between age proportions of colour-ringed choughs and size of feeding flocks within the three core areas used by choughs attending Roosts 1, 2 & 3.

AGE	r	r^2	p	N
		AREA 3 (ROOST 3)	SPRING	
1st	0.431	0.186	0.05	27
2nd	-0.436	0.190	0.05	27
3rd	0.060	0.004	n.s.	27
4th/5th	--	--	--	0
		AREA 3 (ROOST 3)	SUMMER	
1st	-0.279	0.078	0.01	84
2nd	0.606	0.367	0.01	84
3rd	0.096	0.009	n.s.	84
4th/5th	0.059	0.003	n.s.	152
		AREA 3 (ROOST 3)	WINTER	
1st	-0.288	0.083	0.01	100
2nd	0.136	0.018	n.s.	100
3rd	0.353	0.125	0.01	100
4th/5th	0.302	0.091	0.01	200

FIGURE 4.3.1a

Core area 1 - Spring.

Relationship between flock size and the proportion of colour-ringed choughs which were of the four age classes. Sample sizes and means ± 1 s.e. can be found in Appendix 4.

FIGURE 4.3.1b

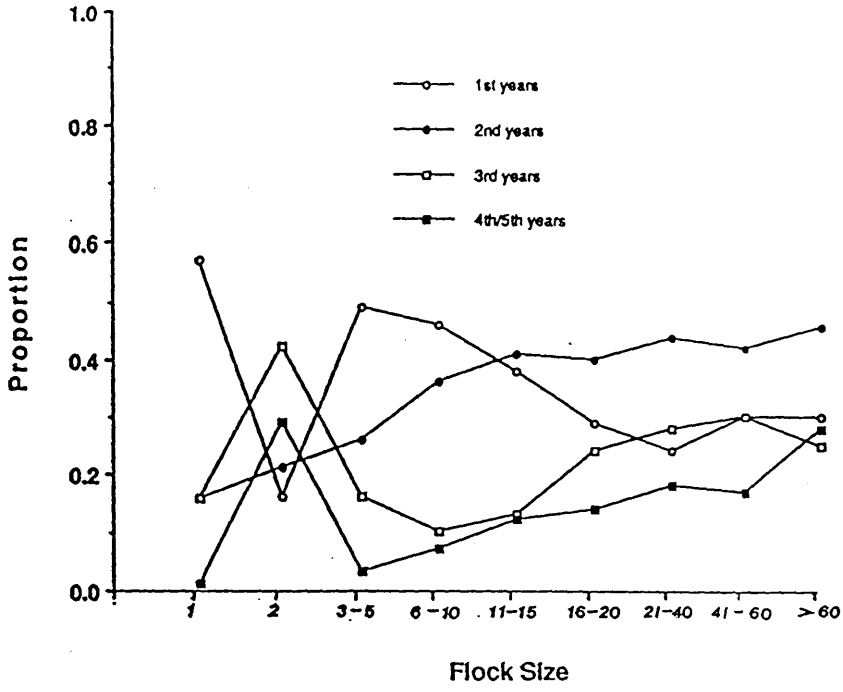
Core area 1 - Summer.

Relationship between flock size and the proportion of colour-ringed choughs which were of the four age classes. Sample sizes and means ± 1 s.e. can be found in Appendix 4.

FIGURE 4.3.1c

Core area 1 - Winter.

Relationship between flock size and the proportion of colour-ringed choughs which were of the four age classes. Sample sizes and means ± 1 s.e. can be found in Appendix 4.


1.0
0.8
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0.4
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0.0
Proportion
1st years
2nd years
3rd years
4th/5th years
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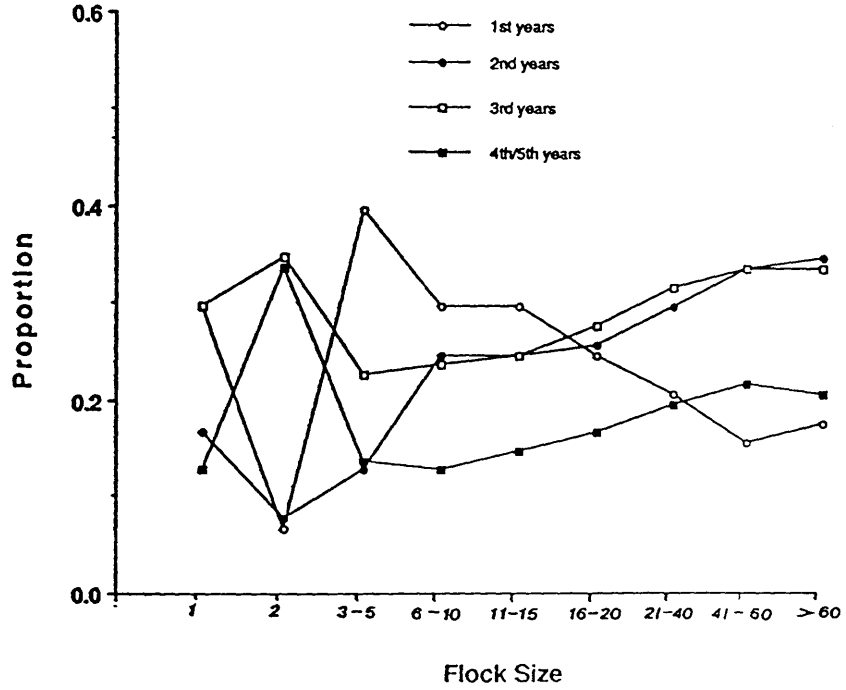
3-5
6-10
11-15
16-20
21-40
41-60
>60
Flock Size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Proportion
1st years
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4th/5th years
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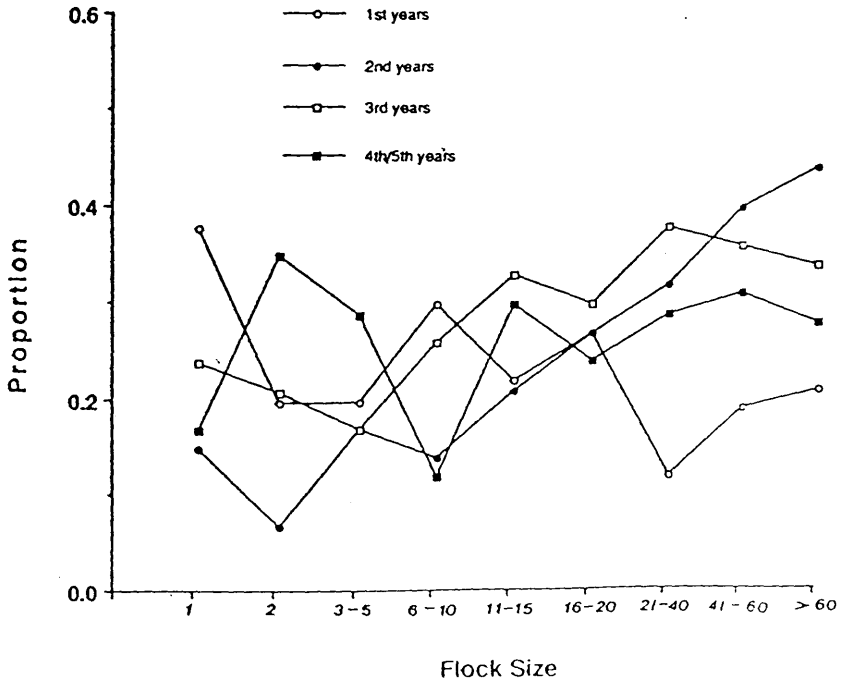
16-20
21-40
41-60
>60
Flock Size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Proportion
1st years
2nd years
3rd years
4th/5th years
1
2
3-5
6-10
11-15
16-20
21-40
41-60
>60
Flock Size

FIGURE 4.3.2a

Core area 2 - Spring.

Relationship between flock size and the proportion of colour-ringed choughs which were of the four age classes. Sample sizes and means ± 1 s.e. can be found in Appendix 4.

FIGURE 4.3.2b

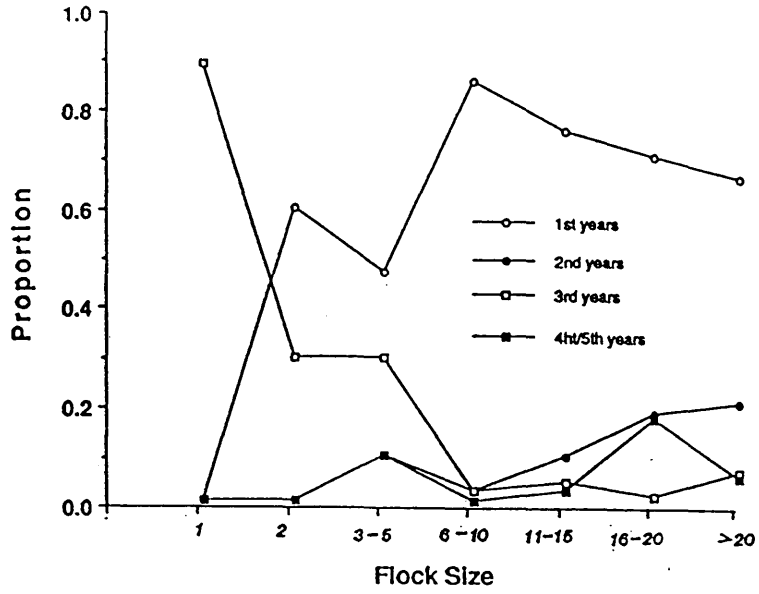
Core area 2 - Summer.

Relationship between flock size and the proportion of colour-ringed choughs which were of the four age classes. Sample sizes and means ± 1 s.e. can be found in Appendix 4.

FIGURE 4.3.2c

Core area 2 - Winter.

Relationship between flock size and the proportion of colour-ringed choughs which were of the four age classes. Sample sizes and means ± 1 s.e. can be found in Appendix 4.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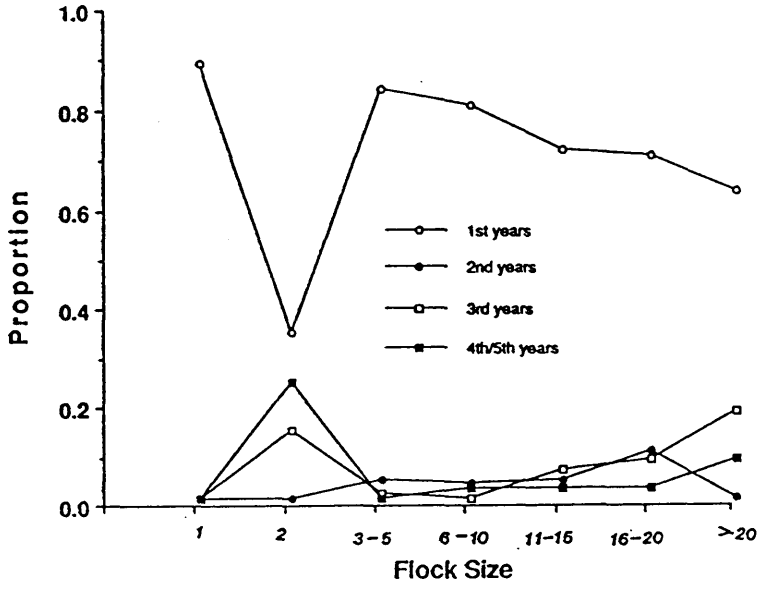
Proportion
1st years
2nd years
3rd years
4ht/5th years
1
2
3-5
6-10
11-15
16-20
>20
Flock Size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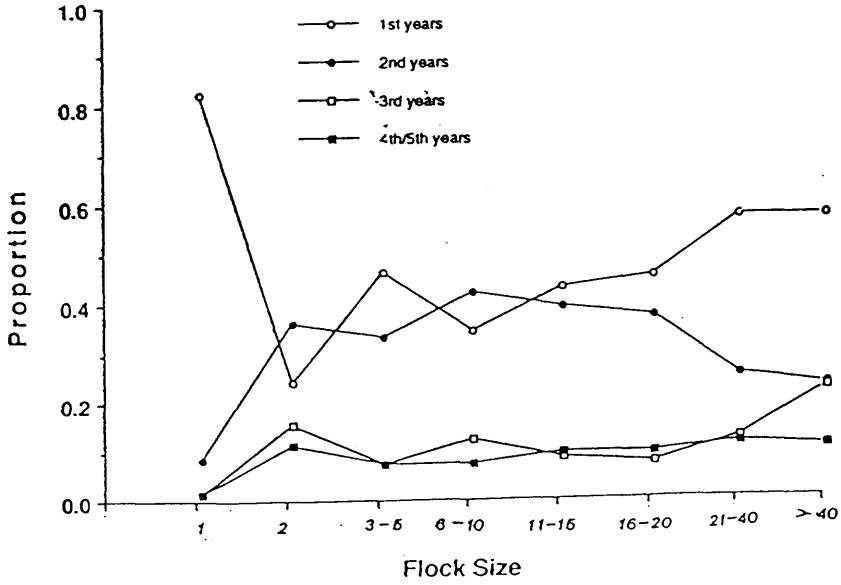
Proportion
1st years
2nd years
3rd years
4th/5th years
1
2
3-5
6-10
11-15
16-20
>20
Flock Size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0.8
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Proportion
1st years
2nd years
3rd years
4th/5th years
1
2
3-5
6-10
11-15
16-20
21-40
>40
Flock Size

FIGURE 4.3.3a

Core area 3 - Spring.

Relationship between flock size and the proportion of colour-ringed choughs which were of the four age classes. Sample sizes and means ± 1 s.e. can be found in Appendix 4.

FIGURE 4.3.3b

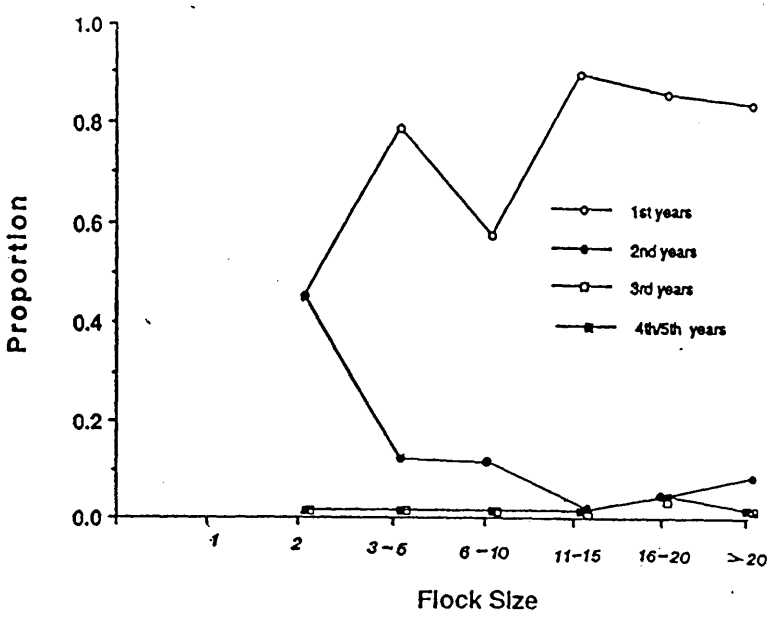
Core area 3 - Summer.

Relationship between flock size and the proportion of colour-ringed choughs which were of the four age classes. Sample sizes and means ± 1 s.e. can be found in Appendix 4.

FIGURE 4.3.3b

Core area 3 - Winter.

Relationship between flock size and the proportion of colour-ringed choughs which were of the four age classes. Sample sizes and means ± 1 s.e. can be found in Appendix 4.


1.0
0.8
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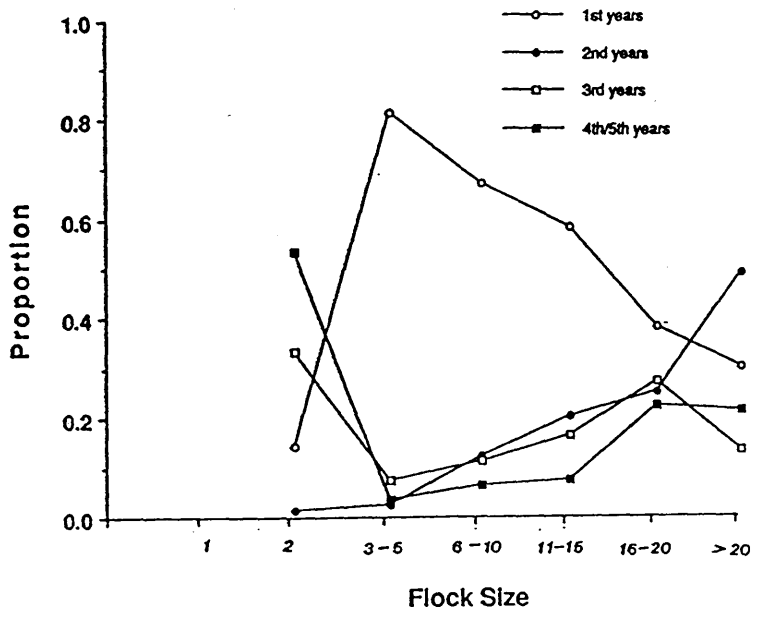
Proportion
1st years
2nd years
3rd years
4th/5th years
1
2
3-5
6-10
11-15
16-20
>20
Flock Size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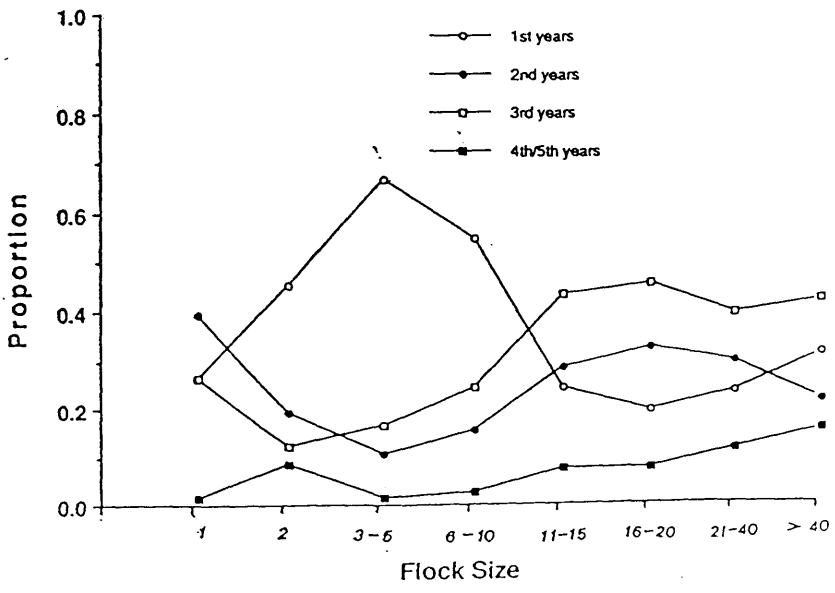
Proportion
1st years
2nd years
3rd years
4th/5th years
1
2
3-5
6-10
11-15
16-20
>20
Flock Size


1.0
0.8
0.6
0.4
0.2
0.0
Proportion
1st years
2nd years
3rd years
4th/5th years
1
2
3-5
6-10
11-15
16-20
21-40
> 40
Flock Size

4.3.4 DISCUSSION.

The results show that there are differences in the age structure of chough flocks depending on the size and location of such flocks. Young birds in general tend to be found in smaller flocks and older birds in larger flocks. From Figures 4.3.1a-c to 4.3.3a-c it is clear that a higher proportion of first years is to be found in the core areas around Roosts 2 & 3. The only time at which young birds are in small flocks is during the summer and winter in core area 3. There is no correlation between flock size and proportion of older birds in core area 2 except for second year birds in the winter where the correlation is high ($r=0.707$). It is difficult to explain this although it may be due to one group of second years from the 1986 cohort which remained together in one large flock in this area where there were fewer older and younger birds in smaller flocks. There is no correlation between flock size and proportion of first year birds in core area 2.

First year choughs may be flocking in small groups of other first years in core areas 1 and 3 either as a function of being pushed out of better feeding sites or by choice. These first years may experience higher rates of aggression than older birds and therefore chose to flock with small numbers of other subordinate first years.

The generally increased proportion of older choughs in large flocks in all areas and in all seasons suggests that there are advantages to these older birds in flocking in larger numbers than first years. They may not experience the same levels of aggression as do younger birds and at the same time incur any other advantages to being in a larger flock (i.e. decreased predation risk and increased food finding chances).

In core areas 2 and 3 where overall there are lower numbers of older birds, there may be no need for first years to form small flocks with other first years. Young

birds in these areas would thus be able to take advantage of being in larger flocks (as for older birds and without the effect of increased aggression from older birds).

The fact that first years move to other areas (section 3.1.7) suggests that these birds may be experiencing competition for food from older birds. Young birds therefore seem to employ two strategies: either flock with small numbers of other young birds, or move to other areas where there are fewer older birds and form larger flocks.

These flocks of young choughs in the population may present problems when using surveys to assess the proportion of young in the entire population since the ability to find these flocks of young birds may make a substantial difference to the estimated overall proportion of young in the population. As young birds also travel further to feed in the winter (section 4.2.3) surveys must include areas distant from the roost. A survey sample from one roost (in this case Roost 1) cannot be used on its own to estimate proportions of different age classes in the population. As seen from the above results, young birds often feed and roost together although separately from many of the older birds, therefore surveys must include as many feeding areas and roosts as possible to get an accurate picture of the age structure of the population. Future conservation policies must take into account this difference in dispersion between age classes. If the conservation of habitat and roost sites becomes an important issue, then it may be necessary to make provision for several suitable areas with adjoining roosts. This would allow the movement of birds to other areas which may be the result of age related dominance within the population.

4.4 VIGILANCE, FEEDING RATES & RATES OF AGGRESSION IN FEEDING FLOCKS.

4.4.1 INTRODUCTION.

Vigilance behaviour has been generally related to predator avoidance (see Introduction 4.1.). Other factors influencing vigilance have not been studied to the same degree (but see Elgar 1989). Of over fifty empirical studies of birds and mammals relating vigilance behaviour and group size, most have found a negative correlation, although many of these relationships show considerable variation which has so far been unexplained. Over 65% of the avian field studies have not controlled for confounding variables such as food density, competition within the feeding group, flock composition, ambient temperature, time of day and distance from cover (Elgar 1989).

As feeding and vigilance behaviour usually cannot be performed at the same time, and as vigilance reduces the time available to feed, one can predict that choughs should try to minimise the time spent vigilant but not to the extent that they increase the risk of predation or competition from conspecifics or other species. Individuals should be able to choose the flock size in which to feed to maximise feeding time although other factors may be important such as social interaction. For example, it may be worth joining a flock where, although feeding time or food intake is reduced, other advantages may be accrued if there is no constraint or pressure to maximise energy intake. This may occur when food is easily obtainable or daylength is not a constraint. Such social advantages may include an increased chance of finding a mate, or learning from other flock members about novel feeding techniques or food sources.

Predators of feeding choughs may include several species of birds of prey. Bullock *et al.* (1983a) stated that feeding choughs take to the wing when ravens *Corvus corax* or peregrine falcons *Falco peregrinus* are present. Although this suggests that they both may be predators of choughs there is little evidence to support this. Ratcliffe (1980) suggests that peregrines probably only take a small number of young although one was seen to kill an adult chough on Islay (C. R. M^{c}Kay pers. comm.). Bullock *et al.* (1983b) suggests that great black-backed gulls *Larus marinus* may be a more significant predator, especially of juveniles. Rolfe (1966) could find no evidence of predation pressure on feeding choughs apart from possibly peregrine falcons. Buzzards flying over feeding choughs often cause them to fly up alarm calling but they were never actually seen to attack choughs. A golden eagle *Aquila chrysaetos* has been seen to attack choughs while at a nest site which was actually located in a communal roost (C. R. M^{c}Kay pers. comm.), although not succeeding in what was a persistent attack. On one occasion a merlin *Falco columbarius* was seen to attack a small flock of young choughs although the merlin was easily avoided and subsequently chased off. It seems unlikely that a small species such as a merlin would seriously attempt to take such relatively large prey. Young choughs after fledging may be more susceptible to attack as they are less manouverable in the air than older choughs.

Human persecution may be a factor in the flocking behaviour of choughs, the human predator maybe treated as any potential avian predator would. Going back through historical records Buchanan (1882) stated that shooting of choughs was a regular occurrence in the process of obtaining "specimens" and urged "proprietors on whose estates this bird still occurs to do all in their power to prevent its extermination". There was little doubt in his mind that the chough had suffered much at that time at the hands of gamekeepers who had "ruthlessly slaughtered it at every opportunity". Ralfe (1905) mentioned that one "trigger-happy gunman" was

able to kill 30 in a morning on the Isle of Man. On Islay itself there is a record of one, if not more choughs being found shot and strung up on a fence as recently as 1982. It seems possible that choughs are still wary of human persecution although not to the same extent as other corvids which are classed as vermin.

4.4.2 METHODS.

Data on vigilance were collected in the form of activity budgets carried out by one minute focal samples on feeding birds. The activities recorded were classed as: a) feeding, when the bird's head was lower than horizontal and the bird was actively foraging. This category also included walking while foraging. b) looking up while feeding or preening, when the bird's head was either horizontal or above the horizontal, c) aggressive interaction which involved displacement of one bird by another either by threat or physical contact (it was impossible to record avoidance behaviour by a focal bird if the focal bird avoided another bird which was out of range of view), d) any other activity such as flying or walking/running when not foraging, preening, allopreening, bathing or loafing. The number of swallows were also recorded although this was more difficult to determine accurately as it depended on observer distance and the type of food items being taken.

Activity budgets were recorded on a hand held tape- recorder and analysed to the nearest second using a digital stopwatch. No more than 5 one minute sample periods of observation were carried out on an individual bird in a particular flock at a particular time and no activity budgets were recorded until one minute after any change in flock size or location had occurred.

Flock size, food items (where possible) and flock composition (determined as the numbers and identities of different age-classes) were also recorded. For the purposes of analyses, food items were classed as either food items from dung, subsoil, or anything else taken (which included surface feeding on grain from stubble or surface feeding for invertebrates). Data on vigilance behaviour were split into dung feeding (a clumped defendable food source), and subsoil feeding which was classed as a more evenly spread, undefendable food source. Data on aggressive interactions were split into interactions while feeding on dung and interactions while feeding on all other food types which included sub-soil feeding.

Observations on first year birds were split into two groups. First year birds were classed as "fledged" after they were no longer in family groups over the period from the start of July until the end of August. "Older" first years were classed as from September onwards to the following July. This split was used to determine any feeding differences between newly fledged independent young and older first years. If this split was not made then one would be combining data from birds which have nearly a year's difference between them. The first few months after independence is the period when feeding skills are developed and thus constraints may be different from those of adults (Buckley & Buckley 1974, Dunn 1972, Davies, 1976, Ricklefs 1979, Moreno 1984, Stevens 1985, MacLean 1986, Walker 1987).

Activity budgets were not recorded for adult birds with dependent young as the constraints and priorities for these birds may be different for non-breeders in the flock (Lazarus & Inglis 1978, Knight & Knight 1986, Caro 1987, Sullivan 1988).

Activity budgets were recorded for fledged young while still with their parents. A comparison is made between the feeding ability of newly fledged choughs while

feeding on easily accessible food items within dung especially dung beetles and their larvae (*Aphodius spp.*) and while feeding on sub-soil invertebrates. The swallow rates, amount of time spent begging, rates of food taken from parents and time spent in other activities are compared on these two food types.

4.4.3 RESULTS.

The mean seconds vigilant / minute in grouped flock sizes for 2nd, 3rd, and 4th/5th years is shown in Figure 4.4.1. Figure 4.4.2 shows the same data for 1st year birds split into "fledged" and "older" birds. The data for Figures 4.4.1 & 4.4.2 are taken from flocks feeding on all types of food items. The results were then split into two types of food item (feeding from dung and sub-soil) and the results shown in Figure 4.4.3 for 2nd, 3rd and 4th/5th years combined and in Figure 4.4.4 for "newly fledged" and "older" first year birds. The corporate vigilance for 2nd, 3rd and 4th/5th year birds (combined from Figure 4.4.3) are shown in Figure 4.4.5. There was a significant negative correlation between flock size and seconds vigilant / minute for all older birds (2nd,3rd, & 4th/5th yrs) on all food types combined (Figure 4.4.1)

The corporate vigilance is shown in Figure 4.4.5 split for birds feeding on dung and sub-soil. Corporate vigilance increased at a higher rate when birds are feeding on dung than sub-soil feeding when flock sizes were greater than 10 (i.e. it reaches the maximum more quickly for choughs feeding on dung than when feeding on subsoil food items.)

The results from Figure 4.4.1 show a typical pattern associated with vigilance and flock size (Pulliam 1973), with the amount of time spent vigilant by individuals decreasing as flock size increases and tailing off after flock sizes of 11-15 birds in

this case. There was a significant negative correlation between flock size and amount of time individuals spent vigilant for all three age classes.

The vigilance pattern of first years choughs, both "old" and "newly fledged" (Figure 4.4 2) was different to that of older birds and showed a decrease in vigilance up to flock sizes 6-10 and 11-15 but after that, increased again as flock size increased. Vigilance levels for "older" first years were consistently lower than that of older birds but increased to a higher level as flock size increased. The vigilance levels of "newly fledged" birds were consistently lower than that of "older" first years.

Data were further examined in relation to two food types. The pattern of vigilance was different for older birds feeding on dung to those feeding on sub-soil food items (Figures 4.4.3). On dung, vigilance levels remained the same as that of birds sub-soil feeding as flock size increased to flock sizes 11-15. Vigilance then increased when flock sizes increased above this level. There was a significant difference in the time spent vigilant on these two food types above flock sizes 11-15 (T-test on unequal variance ($F_{1,3701}$ = 1.15) T = 34.6, d.f. 1124, 2576 $p < 0.001$). The combined data for 2nd,3rd and 4th/5th years is shown in Figure 4.4.4. No analyses could be carried out on first year birds as the results are erratic, suffice it to say that the vigilance levels of "older" first year birds feeding on dung was generally higher than those of birds feeding on sub-soil food items. The same was true of "newly fledged" first years, although vigilance levels while feeding on dung were lower than for "older" birds feeding on sub-soil food items.

Figure 4.4.6 and associated Table 4.4.1 show the number of aggressive interactions of all age classes of birds feeding on dung and all other food types. Data were

combined for groups of flock sizes as sample size were small, and insufficient to enable correlation analysis on individual age classes of choughs. A correlation analysis was carried out however on the combined data for all age classes to show the overall trend. There was a significant positive correlation between flock size and the number of aggressive interactions / minute. From Figure 4.4.6 it is clear that as flock size increased the rate of aggressive interaction also increased with a more marked increase after flock sizes 11-15 when the difference in the aggressive interactions between dung feeding and other food types gets larger. Also, in general aggressive interactions on dung are at a higher level than on other food types (in which sub-soil feeding is include) for all age classes. The results are given in Table 4.4.1.

Vigilance levels were higher while feeding on dung than on sub-soil food and at the same time, rates of aggression were higher while feeding on dung than while feeding on other types of food (which included sub-soil food). Aggression levels increased with flock size at a greater rate while dung feeding than while feeding on other types of food.

Vigilance levels increased with flock size after flock sizes greater than 15 at the same time as rates of aggression increased at a higher rate with flock sizes greater than 15. Rates of aggression were higher for first year birds than for older birds in particular while feeding on dung.

Since first year choughs have low vigilance levels, it may be that older birds do not "trust" them as much as they do older birds and when flocking with first years, older birds may therefore have to spend more time vigilant to account for lower vigilance of first years. Older birds may be able to "judge" the age structure of the

flock in which they are feeding and thus adjust their vigilance levels.

The extent to which vigilance levels of older birds (2nd, 3rd and 4th/5th years) varied with the proportion of first years in the flock was examined. To remove flock size as a factor affecting vigilance, the analysis could only be done with flock size ranges where there was no correlation between flock size and vigilance levels. There were only two flock size groups and ages where there was no correlation between flock size and vigilance; (3rd year birds feeding on dung in flocks 6- 10, flock size v.s vigilance $r=-0.107$ 95 d.f. n.s. and 2nd year birds subsoil feeding in flocks 6-10, flock size vs. vigilance $r=0.049$ 147 d.f. n.s.) there was a significant positive correlation between vigilance levels of adults and the proportion of first years in the flock in both cases ($r=0.44$ 95 d.f. $p < 0.001$ and $r=0.54$ 147 d.f. $p < 0.001$ respectively).

FIGURE 4.4.1

Mean $\pm$ 1 s.e. seconds vigilant for 2nd,3rd and 4th/5th year choughs in flocks of differing size. Data are for choughs feeding on all types of food items.

Sample sizes are displayed for each data point above X- axis in ascending order of age.

regression equation $y = -9.26 \log(x) + 13.74$

$r = 0.93 \quad p < 0.001 \quad 25$ d.f.

Data points for the correlation analysis were the means for each age class in differing flock sizes as shown in the figure.

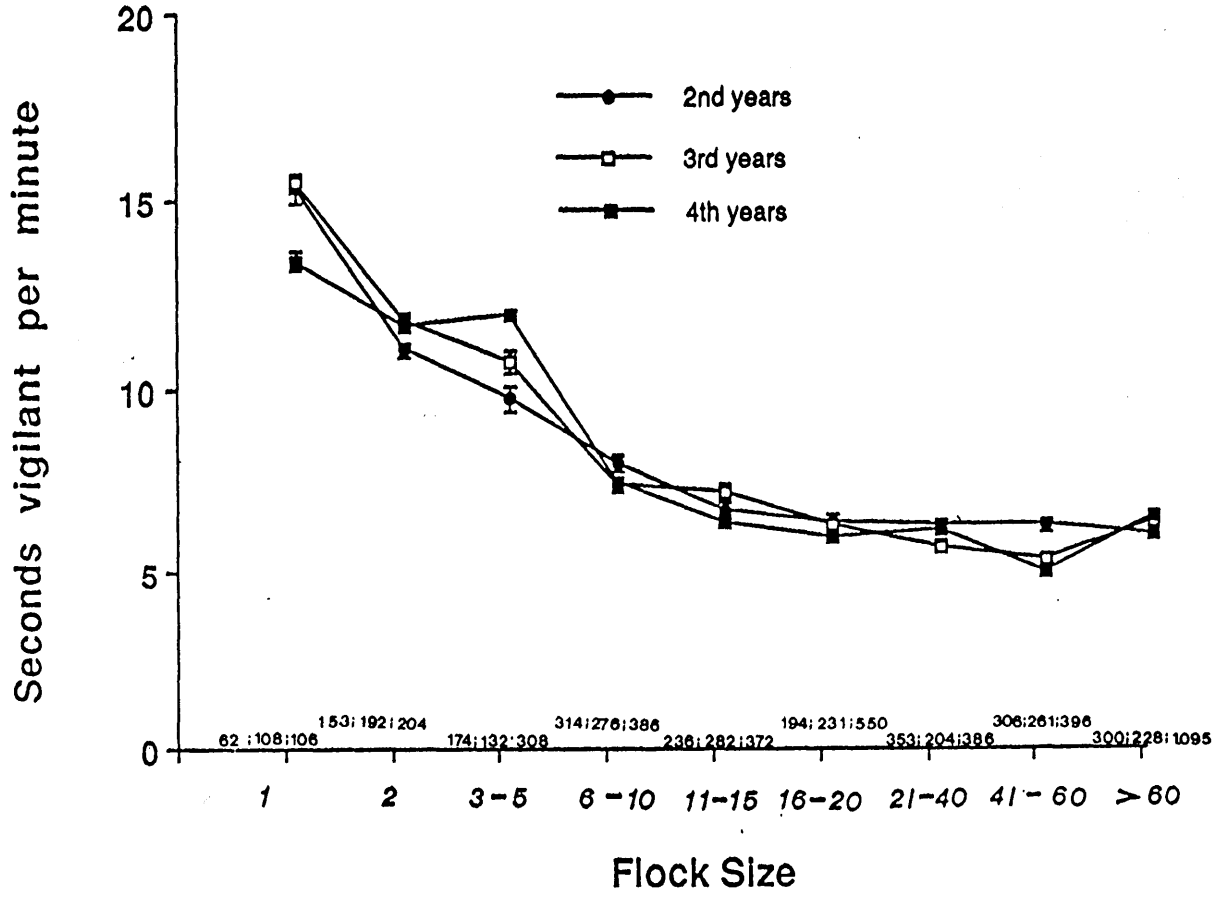

Seconds vigilant per minute
20
15
10
5
0
2nd years
3rd years
4th years
62 ;108;106
153;192;204
174;132;308
314;276;386
236;282;372
194;231;550
353;204;386
306;261;396
300;228;1095
1
2
3-5
6-10
11-15
16-20
21-40
41-60
>60
Flock Size

FIGURE 4.4.2

Mean $\pm$ 1 s.e. seconds vigilant for 1st year choughs in differing flock sizes. Data are split into "newly fledged" and "older" classes of 1st years. A full explanation of these two age categories can be found in the text (Section 4.4.2).

Data are for first years choughs feeding on all types of food items.

Sample size is shown beside the relevant data point.

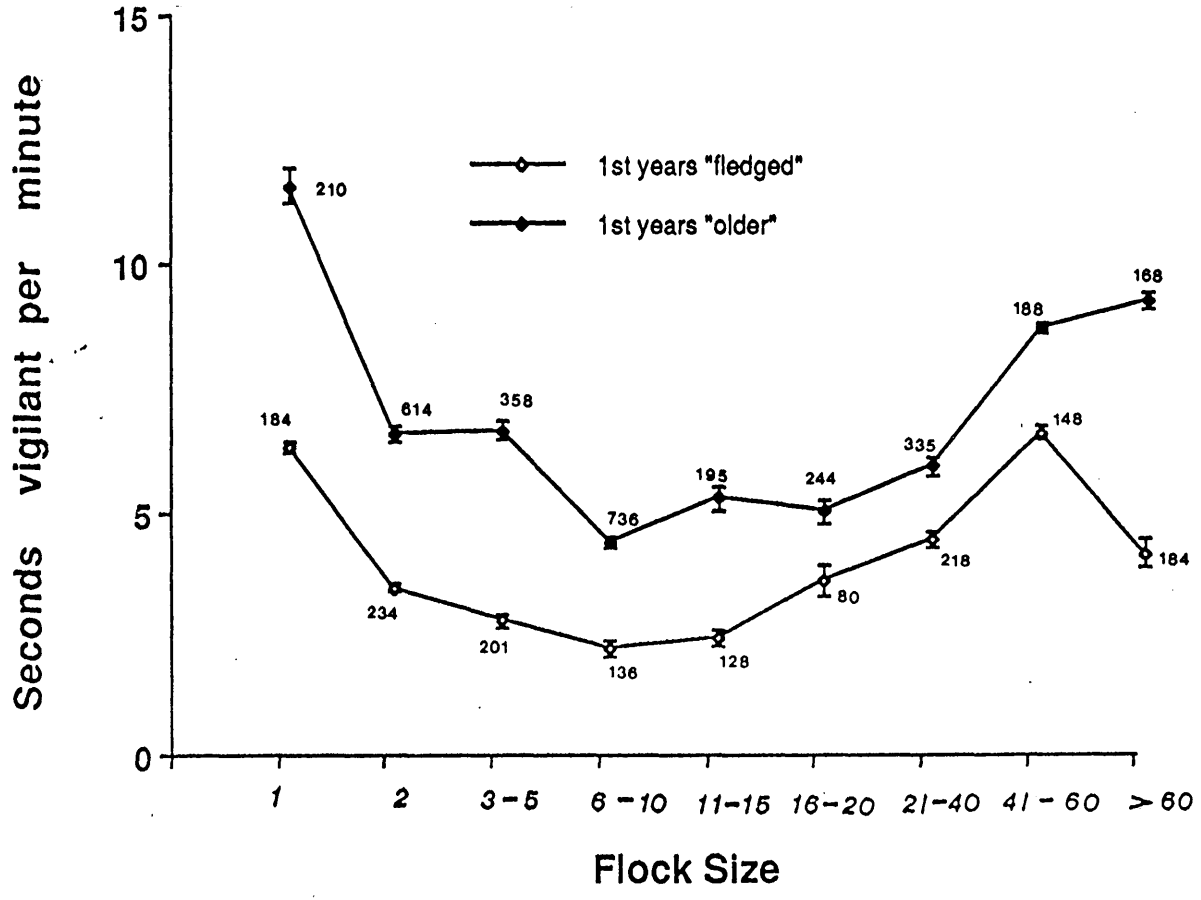

15
10
5
0
Seconds vigilant per minute
1st years "fledged"
1st years "older"
210
614
358
736
195
244
335
188
168
184
234
201
136
128
80
218
148
184
1
2
3-5
6-10
11-15
16-20
21-40
41-60
>60
Flock Size

FIGURE 4.4.3

Mean $\pm$ 1 s.e. seconds vigilant per minute for 2nd, 3rd and 4th/5th years combined in flocks of differing size. Data are split into dung feeding and sub-soil feeding. Sample size is shown beside the relevant data point.

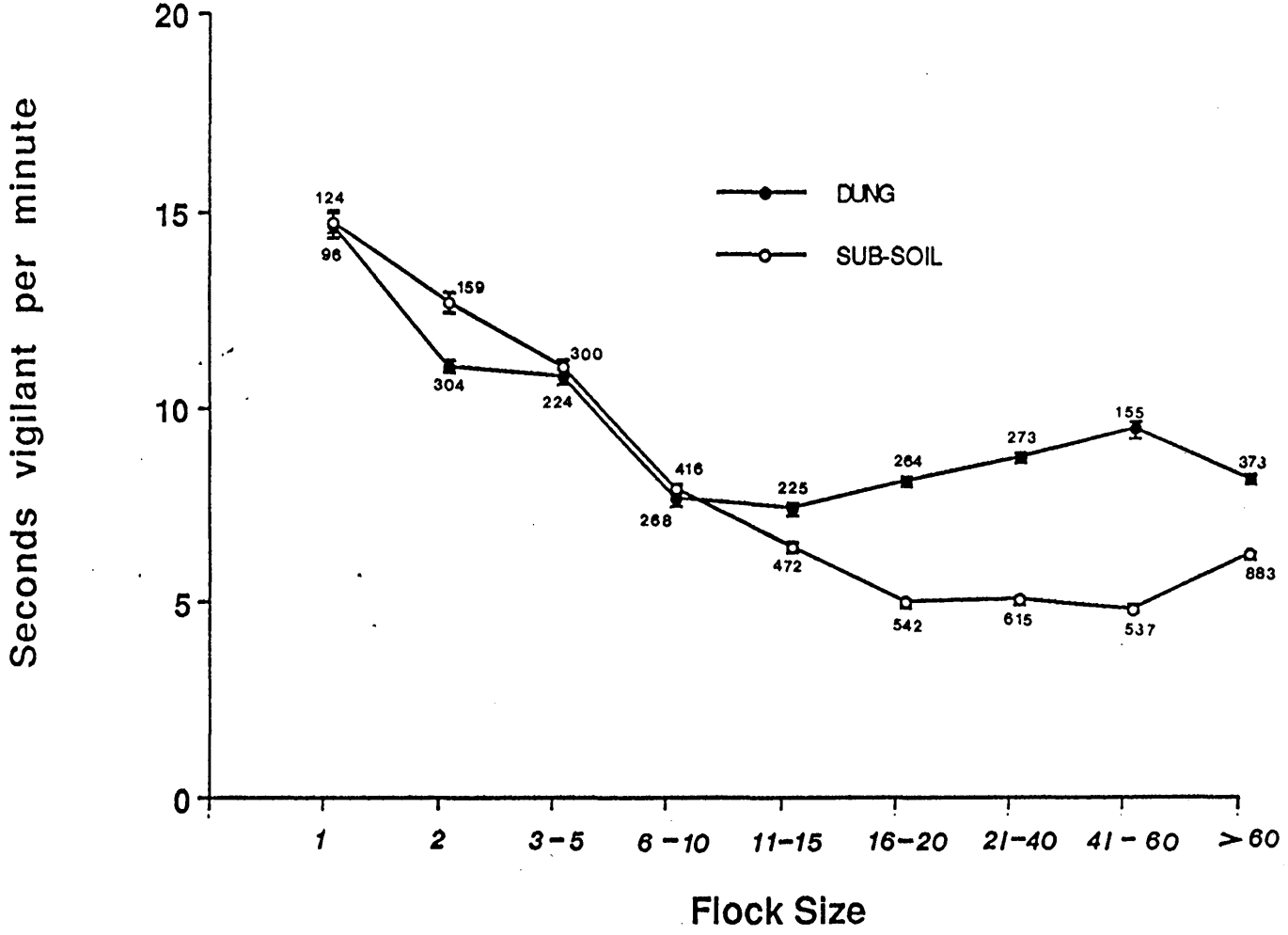

Seconds vigilant per minute
20
15
10
5
0
DUNG
SUB-SOIL
124
96
159
304
300
224
416
268
225
472
264
542
273
615
155
537
373
883
1
2
3-5
6-10
11-15
16-20
21-40
41-60
>60
Flock Size

FIGURE 4.4.4

Mean ± 1 s.e. seconds vigilant per minute for first year choughs split into two food types; dung and sub-soil.

Data are shown for "newly fledged" and "older" first year choughs. A full explanation of these two age categories can be found in the text (Section 4.4.2). Sample size is shown beside the relevant data point.

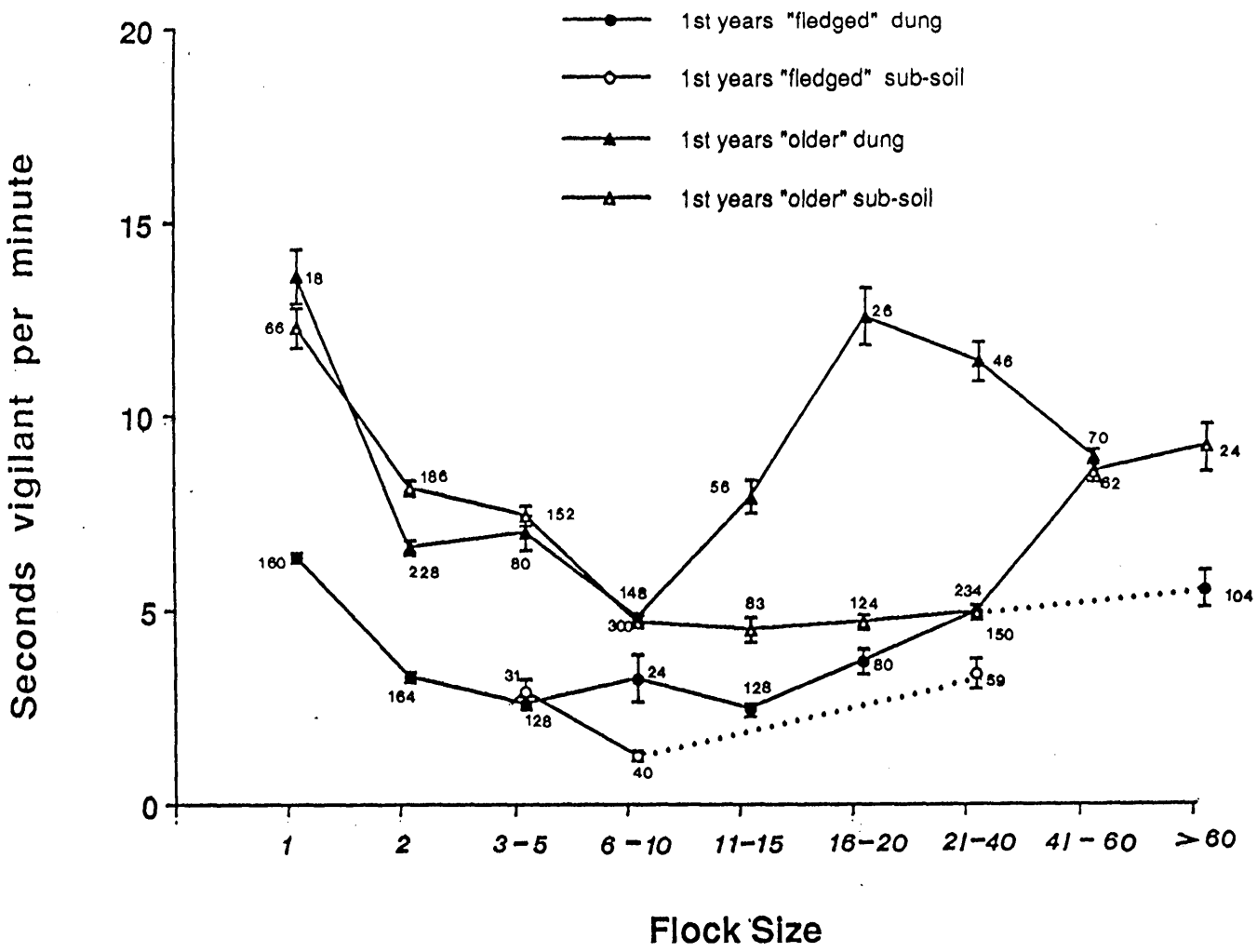

1st years "fledged" dung
1st years "fledged" sub-soil
1st years "older" dung
1st years "older" sub-soil
Seconds vigilant per minute
20
15
10
5
0
1
2
3-5
6-10
11-15
16-20
21-40
41-60
>60
Flock Size
18
66
186
228
152
80
148
300
56
26
83
124
46
70
62
24
160
164
31
128
24
40
128
80
234
150
59
104

FIGURE 4.4.5

Corporate vigilance of 2nd, 3rd and 4th/5th year choughs in differing flock sizes. Vigilance data used in the calculation are the mean for the above age classes combined. Data from first year choughs were not used in the calculation as the vigilance levels differed from that of older choughs. Flock size used in the calculation was the mean of each flock size category (for flocks greater than 2). The data are split to show corporate vigilance levels on two food types; dung and sub-soil. The equation used to calculate the corporate vigilance is given below.

$$\text{corporate vigilance} = 1 - (1 - V_n)^n$$

where V = proportion of time spent vigilant

n = flock size.

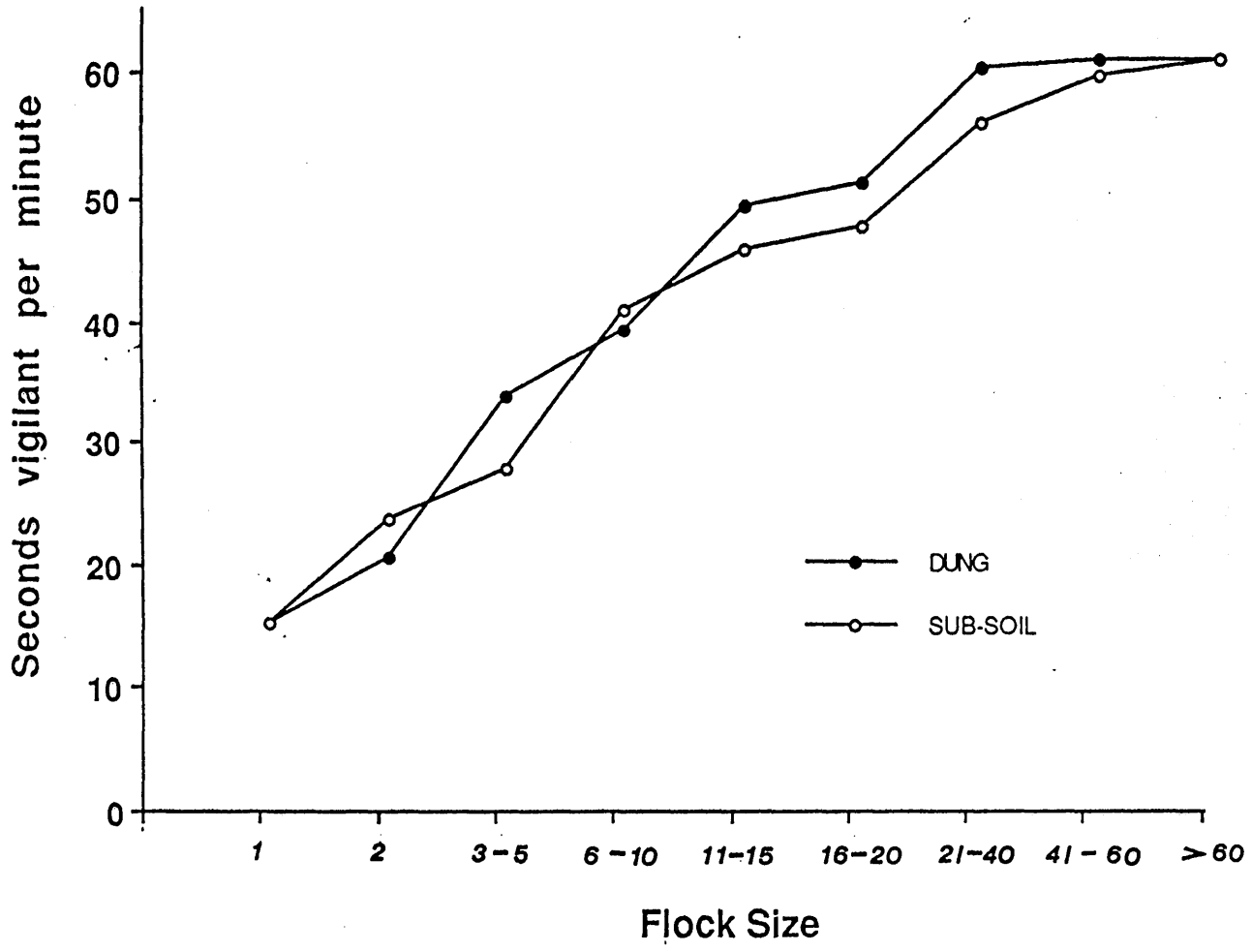

Seconds vigilant per minute
0
10
20
30
40
50
60
1
2
3-5
6-10
11-15
16-20
21-40
41-60
>60
Flock Size
DUNG
SUB-SOIL

FIGURE 4.4.6

The rate of aggressive interaction in differing flock size. Data are shown for number of aggressive interactions divided by number of minute samples on focal birds of each age class (i.e. aggressive interactions per age-class per minute). Data shown are for 2nd, 3rd and 4th/5th years combined and for "newly fledged" and "older" first years. Data for the above age classes is split into two food types; dung feeding and feeding on all other food types combined (this category includes sub-soil feeding).

Sample sizes can be found in Table 4.4.1.

regression equation $y = 0.01x - 0.01$

$r = 0.88$ $p < 0.001$ 42 d.f

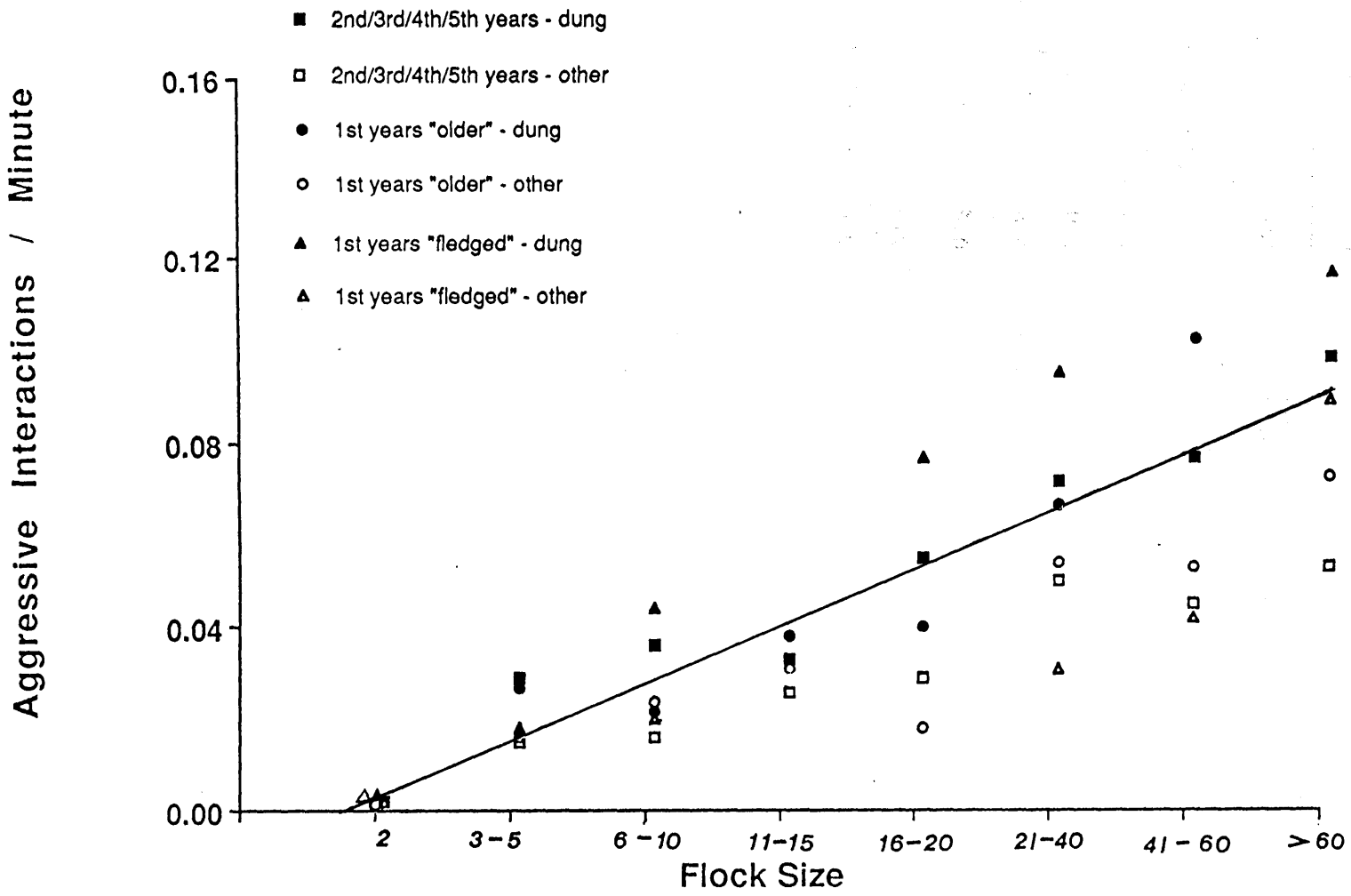

2nd/3rd/4th/5th years - dung
2nd/3rd/4th/5th years - other
1st years "older" - dung
1st years "older" - other
1st years "fledged" - dung
1st years "fledged" - other
Aggressive Interactions / Minute
0.16
0.12
0.08
0.04
0.00
2
3-5
6-10
11-15
16-20
21-40
41-60
>60
Flock Size

Table 4.4.1. Rates of aggression classed as the number of aggressive interactions choughs of different ages were involved in when the subject of focal samples. Results are given for choughs feeding on two types of food item (dung feeding and other food types) as number of aggressive interactions divided by the total number of one minute focal sample observations (i.e. aggressive interactions per minute). Older birds are a combination of data for 2nd, 3rd and 4th/5th years. Sample sizes are shown in brackets.

INTERACTIONS/MINUTE

1ST YEARS "NEWLY FLEDGED"

FLOCK SIZE	FOOD TYPE: DUNG	FOOD TYPE: OTHER FOOD
2	0.000 (164)	0.000 (70)
3-5	0.016 (128)	0.014 (73)
6-10	0.042 (24)	0.018 (112)
11-15	0.031 (228)	--
16-20	0.075 (80)	--
21-40	0.093 (150)	0.029 (68)
41-60	--	0.040 (148)
> 60	0.115 (104)	0.087 (80)

1ST YEARS "OLDER""

FLOCK SIZE	FOOD TYPE: DUNG	FOOD TYPE: OTHER FOOD
2	0.000 (228)	0.000 (413)
3-5	0.025 (80)	0.014 (278)
6-10	0.020 (148)	0.022 (588)
11-15	0.036 (56)	0.029 (139)
16-20	0.038 (26)	0.016 (128)
21-40	0.065 (46)	0.052 (289)
41-60	0.100 (70)	0.051 (118)
> 60	--	0.071 (168)

Table 4.4.1 cont. Rates of aggression classed as the number of aggressive interactions choughs of different ages were involved in when the subject of focal samples. Results are given for choughs feeding on two types of food item (dung feeding and other food types) as number of aggressive interactions divided by the total number of one minute focal sample observations (i.e. aggressive interactions per minute). Older birds are a combination of data for 2nd, 3rd and 4th/5th years. Sample sizes are shown in brackets.

INTERACTIONS/MINUTE

OLDER BIRDS (2nd,3rd,4th & 5th yrs)

FLOCK SIZE	FOOD TYPE: DUNG		FOOD TYPE: OTHER FOOD	
2	0.000	(304)	0.000	(245)
3-5	0.027	(224)	0.013	(390)
6-10	0.034	(268)	0.014	(708)
11-15	0.031	(225)	0.024	(665)
16-20	0.053	(264)	0.027	(711)
21-40	0.070	(159)	0.048	(688)
41-60	0.075	(159)	0.043	(808)
> 60	0.096	(343)	0.051	(1250)

Feeding rates (i.e. the number of swallows per minute) were analysed in relation to flock size and on two types of food item (sub-soil and dung feeding). There was no correlation between flock size and swallows per minute for older birds feeding on dung or for "older" fledged first years, (Figure 4.4.7). "Newly fledged" first years feeding on dung showed a decrease in swallows per minute when flock size was greater than 60. Although the relationship is significant, ($r = -0.26$, d.f.937) , the coefficient of determination ($r^2 = 0.07$) is small, and not much of the variation is explained; the decrease in swallows per minute was not constant and only obvious after flock sizes of 60. The number of swallows per minute when sub-soil feeding (Figure 4.4.8) was lower for "newly fledged first years than for "older" first years and for older choughs. There were too few data to make any statistical comparisons as "newly fledged birds were seldom found feeding on sub- soil food items.

The number of swallows per minute may be a factor purely of the actual amount of time within a minute which the bird spends feeding. For example, a bird which only spent 30 seconds feeding and swallowed three items within the 30 seconds would have the same swallows per minute as a bird which spent one minute feeding but still only swallowed three items within that minute. In fact, the bird which swallows three items in one minute but is only spending 30 seconds to obtain these actually has double the feeding rate than a bird which takes one minute of feeding to also swallow three items.

To take account of this, the actual swallows per amount of time spent feeding was also analysed (swallows per focal minute divided by time spent feeding per minute) This can then be converted to swallows per minute by multiplying by 60. The results are shown in Figure 4.4.9 for dung feeding and Figure 4.4.10 for subsoil feeding. The swallows per time spent feeding on dung increase up to flock sizes 3 -

5 but then level off for older birds. "Newly fledged" birds' swallows per minute feeding decreased when flock size was greater than 60. The null hypothesis is that swallows per time spent feeding should be independent of other activities such as vigilance as flock size changes. This suggests that any decrease in swallows per unit time spent feeding must be accounted for by other factors such as interruptions during feeding (i.e. vigilance or competition disrupting the feeding of birds and thus lowering the actual swallows per time spent feeding).

For all ages, the number of swallows per unit time spent feeding increases with flock size up to flock sizes 3 - 10 for all ages of bird feeding on dung (Figure 4.4.9 and also for older birds and "older" first years feeding on sub-soil food, (Figure 4.4.10). The data are rather fragmented for "newly fledged" birds feeding on sub-soil food items, therefore it is impossible to draw any comparisons other than the swallows per time spent feeding is consistently lower than that of older birds.

The amount of time spent begging and feeding, the swallows per minute and swallows per unit time spent feeding was examined for fledged choughs still with their parents in feeding flocks. The number of items swallowed when food was given by parents and the amount of time spent in other activities (inactive, preening, moving and any other activity) was also examined . There was no correlation between any of these activities and flock size. Data were compared for newly fledged birds with their parents while dung feeding and sub-soil feeding. The results are shown in Table 4.4.2.

Newly fledged choughs spent significantly less time begging and involved in "other activities" when with their parents feeding on dung than newly fledged birds with parents feeding on sub-soil food. Young birds had a higher number of swallows per minute and swallows per time spent feeding when they were feeding on dung. They also took fewer items of food from their parents. Young birds also spend

significantly more time feeding themselves while feeding on dung than while sub-soil feeding.

FIGURE 4.4.7

Swallows per minute for choughs feeding on dung in differing flock sizes. Data are shown for 2nd, 3rd and 4th/5th years combined and for "newly fledged" and "older" first year choughs.

Sample size is shown beside the relevant data point.

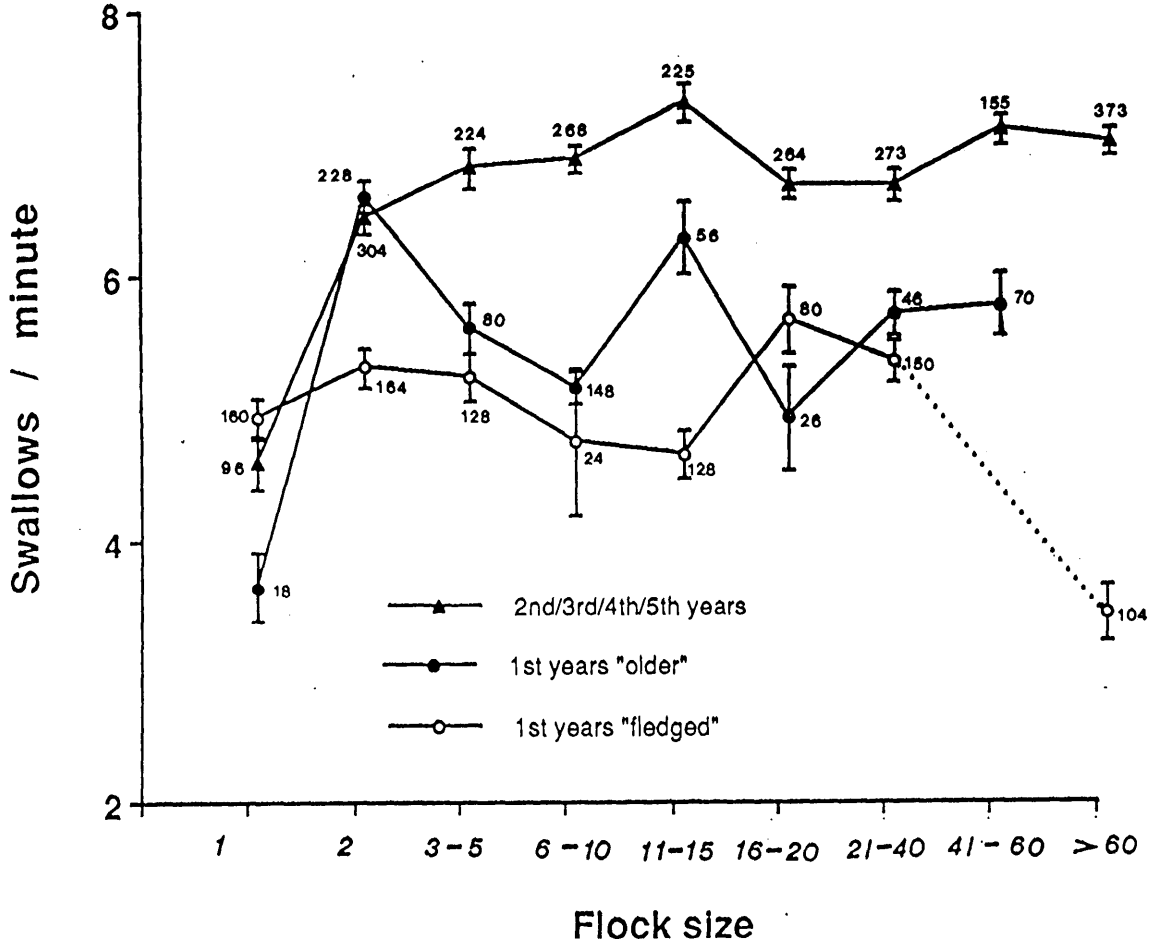

Swallows / minute
8
6
4
2
225
224
266
264
273
155
373
228
304
56
80
148
80
46
70
160
164
128
24
128
26
150
96
18
104
2nd/3rd/4th/5th years
1st years "older"
1st years "fledged"
1
2
3-5
6-10
11-15
16-20
21-40
41-60
>60
Flock size

FIGURE 4.4.8

Swallows per minute for choughs feeding on sub-soil food items in differing flock sizes. Data are shown for 2nd, 3rd and 4th/5th years combined and for "newly fledged" and "older" first year choughs. Sample size is shown beside the relevant data point.

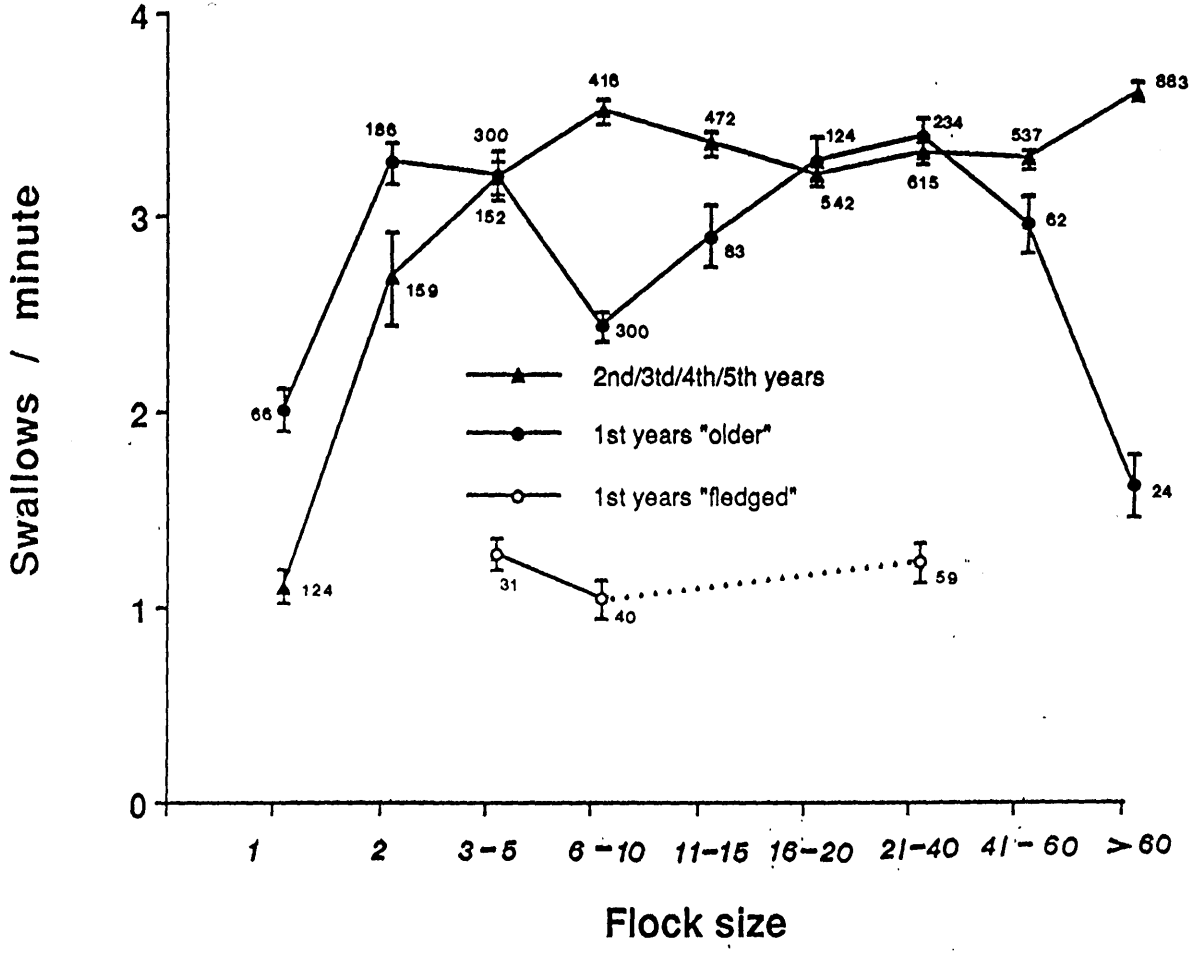

Swallows / minute
4
3
2
1
0
66
186
300
416
472
124
234
537
883
124
159
152
300
83
542
615
62
24
31
40
59
2nd/3td/4th/5th years
1st years "older"
1st years "fledged"
1
2
3-5
6-10
11-15
16-20
21-40
41-60
>60
Flock size

FIGURE 4.4.9

Swallows per time spent feeding (X 60 to convert to equivalent swallows per minute) for choughs feeding on dung in differing flock sizes. Data are shown for 2nd, 3rd and 4th/5th years combined and for "newly fledged" and "older" first year choughs.

Sample size is shown beside the relevant data point.

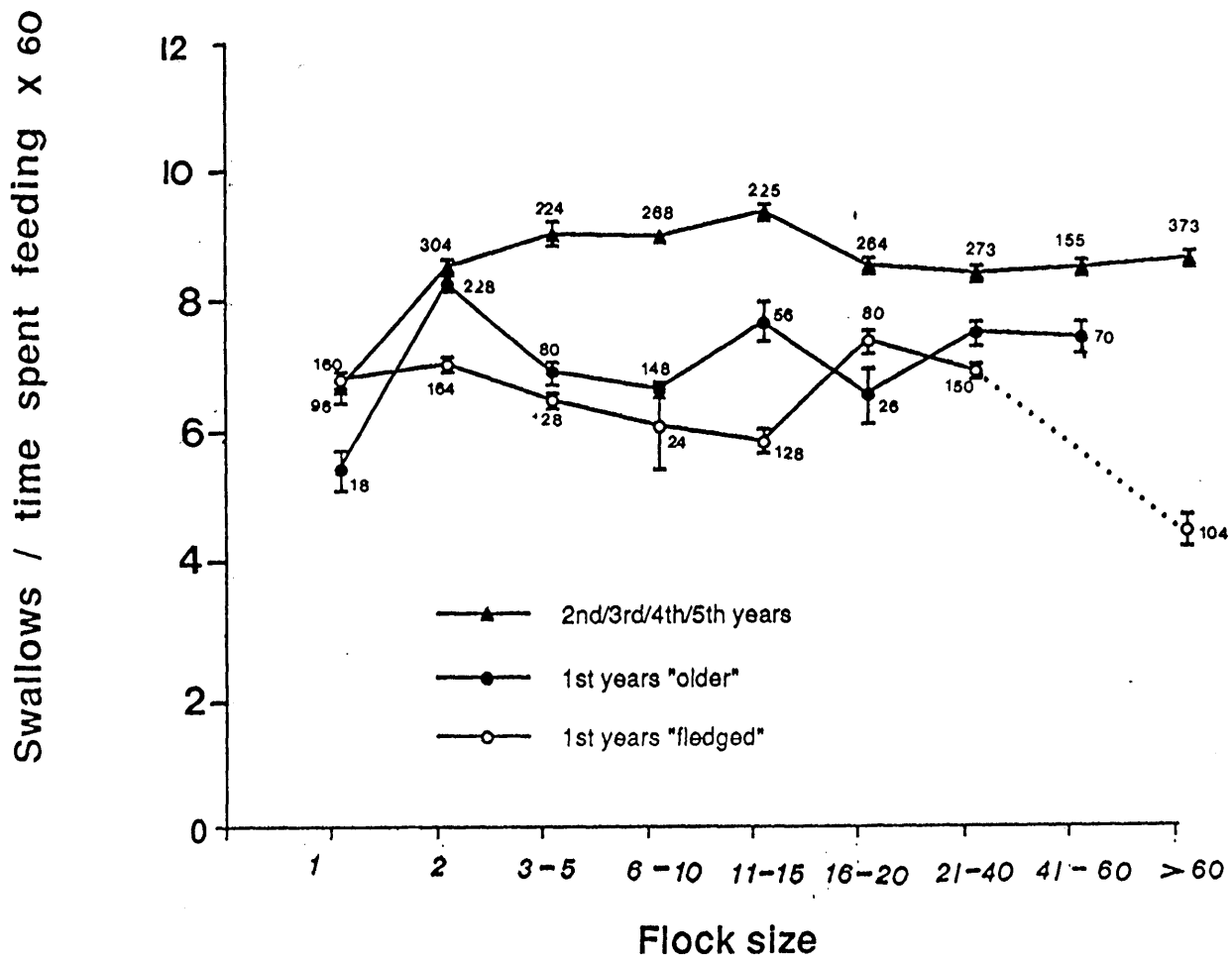

Swallows / time spent feeding x 60
12
10
8
6
4
2
0
304
224
268
225
264
273
155
373
228
160
80
148
56
80
70
98
164
128
24
128
26
150
18
104
2nd/3rd/4th/5th years
1st years "older"
1st years "fledged"
1
2
3-5
6-10
11-15
16-20
21-40
41-60
>60
Flock size

FIGURE 4.4.10

Swallows per time spent feeding (X 60 to convert to equivalent swallows per minute) for choughs feeding on sub-soil food items in differing flock sizes. Data are shown for 2nd, 3rd and 4th/5th years combined and for "newly fledged" and "older" first year choughs.

Sample size is shown beside the relevant data point.

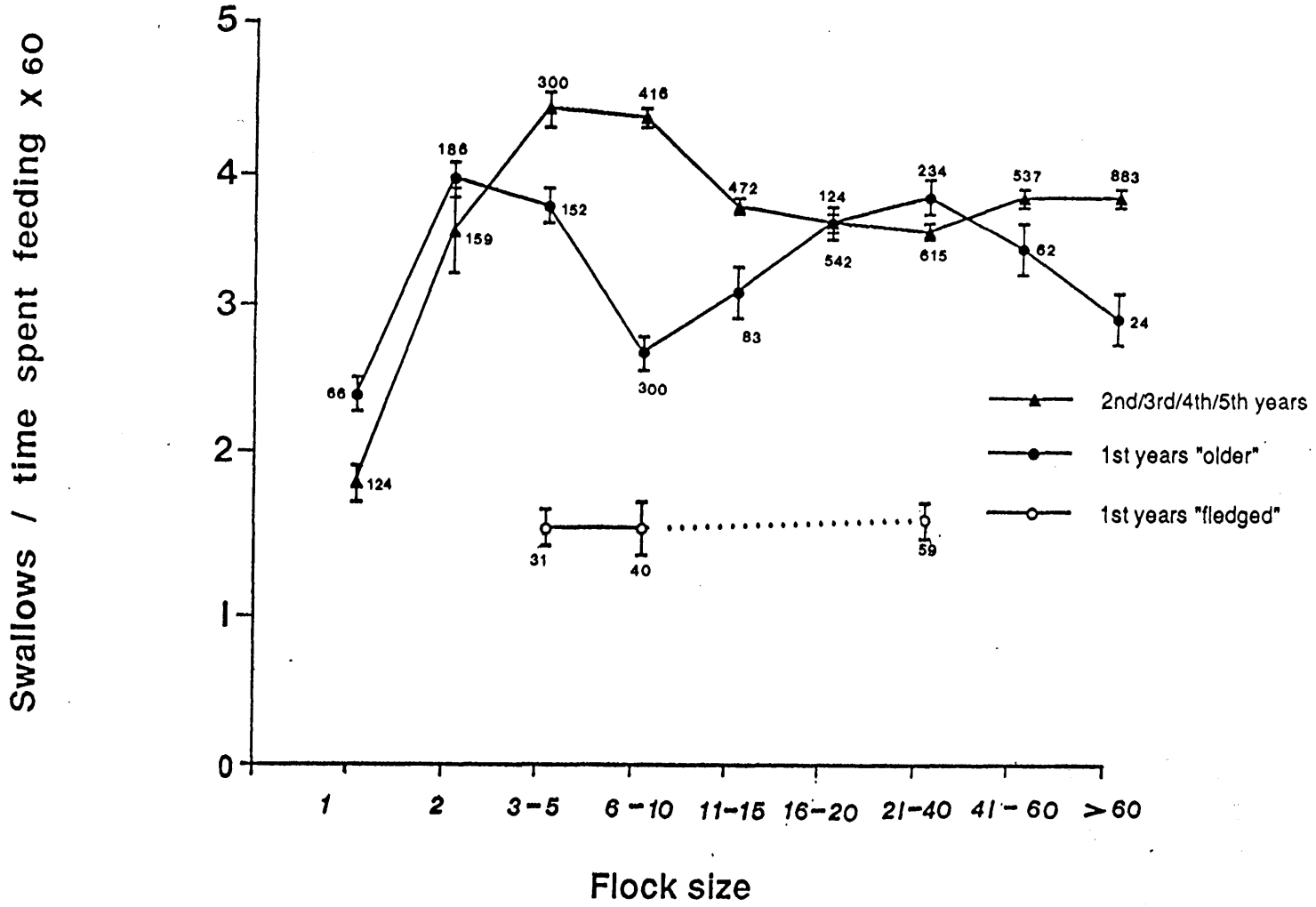

Swallows / time spent feeding x 60
5
4
3
2
1
0
300
416
186
472
124
234
537
883
152
159
542
615
62
24
66
300
83
124
31
40
59
2nd/3rd/4th/5th years
1st years "older"
1st years "fledged"
1
2
3-5
6-10
11-15
16-20
21-40
41-60
>60
Flock size

Table 4.4.2. The mean ± s.e. seconds per minute in different activities is shown for fledged choughs while with their parents and feeding on dung and sub-soil feeding. Significance levels and sample sizes are given. Analysis was by T-test (2593 d.f. for all test pairs).

	FOOD TYPE				
	DUNG N=1169		SUB-SOIL N=1426		
	mean	s.e.	mean	s.e.	
BEGGING	14.59	0.41	27.54	0.47	T=-20.63 p < 0.001
FEEDING	29.24	0.44	8.44	0.28	T=39.74 p < 0.001
SWALLOWS/ MINUTE	2.92	0.07	0.10	0.01	T=38.42 p < 0.001
SWALLOWS/ UNIT TIME FEEDING (X60)	4.86	0.48	0.24	0.02	T=49.24 p < 0.001
ITEMS TAKEN FROM PARENTS /MINUTE	0.70	0.03	0.94	0.02	T=-6.72 p < 0.001
OTHER ACTIVITIES	13.87	0.37	22.74	0.46	T=-14.60 p < 0.001

4.4.4 DISCUSSION.

Choughs showed the typical pattern of vigilance behaviour when they were over one year old. That is, individuals spent less time vigilant as flock size increased. Therefore it is an advantage for choughs to be in larger flocks as the amount of time spent vigilant for individuals decreases but overall corporate vigilance increases to eventually reach 100% vigilance. This means that there will always be at least one bird vigilant when the corporate vigilance is 100%.

For first year birds, vigilance levels were lower than those of older birds and decreased with flock size but only up to flock sizes 6-15; after this, vigilance levels increase again on both dung and other types of food. That vigilance levels of young birds are lower than those of older birds been noted by several authors (eg. Owen 1972, Heinsohn 1987, Hogstad 1988, Sullivan 1988). Heinsohn (1987) suggested that higher scanning rates by older birds in small groups of cooperatively breeding white-winged choughs *Cocorax melanorhamphos* may be in compensation for the less efficient foraging of younger birds that therefore have less time for vigilance. Older choughs were shown to adjust (increase) their vigilance levels when feeding with a high proportion of young choughs. One might expect this result to occur only in small flocks because as flock size increases the pressure on only a few older birds may be lessened the numbers of others present, thus taking the responsibility of vigilance away from the few older birds. Older choughs may have to decide whether to flock with young choughs and maintain higher vigilance levels but be able to gain the best feeding sites due to their greater dominance, or to feed with other older choughs, reduce their vigilance levels but maybe experience more competition for food. Young choughs too may be able to adjust their levels of vigilance. Sullivan (1988) found that the scanning rates of fledgling yellow-eyed juncos *Junco*

phaeonotus increased with age and were higher in flocks of juveniles than when feeding with parents. It may be that young choughs could take advantage of flocking with older birds as this would allow them to spend more time feeding. There would come a stage as flock size increased however, when the rates of aggression directed towards these young choughs would become disadvantageous. The fact that young yellow-eyed juncos can adjust their scanning rate when with other young birds suggests that young birds are capable of adjusting their vigilance levels.

Vigilance levels were at their lowest for first year choughs in smaller flocks and as the results of section 4.3.3 suggest first year birds tend to be found in smaller flocks, especially in areas where there is a larger proportion of older birds. In the cases where first year birds were found in larger flocks, these flocks tended to have a high proportion of first years and in areas (especially core areas 2 & 3) where there was a low proportion of older birds. First year birds in Area 1 where there was a higher proportion of older birds tended to be found in smaller flocks.

Food type seems to play an important role in the vigilance behaviour of choughs. On dung, which can be thought of as a patchy food source and which may be worth defending, vigilance levels were higher overall and increase as flock size increases past 11-15 birds. This suggests that vigilance was not purely anti-predator in function but may be due to an increase in the need to be aware of potential aggression from other flock members (Knight & Knight 1986).

Rates of aggression increased with flock size. Risenhoover & Bailey (1985) found that rates of aggression actually decreased with increased group size in mountain goats *Oreamnos americanus* and related this to a switch in behaviour as group size increased from frequent agonistic behaviour to "scramble" competition as defence of

a good feeding site was less profitable with increased group size. This type of scramble competition is not seen in choughs. This may be because large groups of mountain goats contain closely related individuals which maintain close social bonds, unlike large flocks of choughs which to the best of our knowledge are not closely related although family and sibling members do occur within larger flocks.

Young choughs experience a greater rate of aggressive interaction than older choughs with the degree of difference between dung and other food types increasing with increased flock size.

First year choughs in flocks greater than 15 had higher interaction rates than older birds. As interaction rates are higher on dung this suggests that this is a food source which is worth competing for and defending. As a suitable cow pat contains more than one item of easily accessible food then competition may be more fierce than on subsoil food which is not defendable and can be swallowed by a subordinate bird before being taken by another. Holyoak (1972) suggested that the low levels of aggression seen by him in feeding flocks of choughs were attributable to the small size of the food items they usually took, it being pointless for one chough to try to displace another at food if the threatened bird could swallow the disputed item. Warnes (1983a) noted aggression while choughs were feeding on dung.

The lower rates of aggression and vigilance while birds were feeding on food other than dung suggest that increased vigilance by young birds which were feeding on other food types, in this case sub-soil food which is cryptic, is not related wholly to looking up to avoid aggression but may be due to observational learning.

Young choughs may not need to learn from other choughs while feeding on dung as they are quite successful (although less so than older choughs) while still with their parents. Young choughs may also improve their foraging techniques by

forming a preference for commonly encountered food types (Capretta 1969, Rabinowitch 1969) and as such may depend more on dung than older birds with improved foraging skills to provide enough food for their survival.

For a young chough in its first year the choices of which is the best flock size and flock composition to be in may be crucial to its survival if competition for food and/or avoiding predators are important factors. Young choughs have higher swallow rates on dung and can feed independently of their parents than when the family group is feeding on sub-soil invertebrates. As young birds can easily obtain food from dung, this may be an important food resource as they develop, giving them time to increase feeding skills on other food sources. These feeding skills may be developed by observational learning (Klopfer 1961, Galef 1976) which may account for an increase in vigilance with flock size on sub-soil where competition may not play such an important role. Young choughs may trade off the disadvantage of increased aggression when feeding on dung with an increase in their food intake on an easily obtainable food source. They may join flocks feeding on sub-soil food items to improve their feeding techniques by observational learning. Another choice open to first year choughs is to move to an area where there are fewer older birds and where consequently competition for food, especially easily obtainable food sources such as dung are available. This pattern seems to be occurring with high proportions of young choughs being found in flocks in areas with fewer older birds, (core areas 2 & 3, see section 4.3.3). This has been observed by several authors for rooks and starlings (Dunnet *et al.* 1969, Henty 1989). They also have the choice of forming small flocks with a high proportion of young in areas where there are a larger number of older birds and thus avoiding competition from older birds. This strategy seems to be in operation in core area 1 for young choughs, especially during the winter when competition for food may be at its highest for them, and young choughs are found in smaller flock sizes and further from the roost than older choughs. Young choughs which move to other areas are

found in larger flocks which contain lower proportions of older birds. The fact that these young choughs are found in larger flocks could be the result of several factors. They may join other young choughs which have lower dominance status. Young choughs may therefore experience a lower rate of aggression towards them in a large flock of young choughs than in a comparable flock size which contains a higher proportion of older choughs. Young choughs may also flock together in larger flocks in separate areas to older choughs purely as a result of finding themselves in poorer feeding habitat (which is perhaps why older birds do not use the area). These young choughs may be forced to congregate in the few available feeding areas.

In summary:-

Older choughs displayed the typical pattern of vigilance behaviour with a decrease in vigilance of individuals as flock size increases.

First year choughs had lower vigilance levels than older choughs up to flock sizes of 11-15. After this, vigilance levels increased and reach higher levels than those of older birds. Observational learning on cryptic food items (eg. subsoil food items), or vigilance for competition from older choughs while feeding on discrete patches of defendable food such as dung may account for this.

The rate of aggressive interactions was higher while feeding on dung (defendable food source) than while feeding on sub-soil food items (single, un-defendable food).

First year choughs experienced a higher rate of aggressive interaction than older choughs, in particular in large flocks and when feeding on dung.

Swallow rates were lower for first year choughs while feeding on subsoil food items than for older choughs. Although swallow rates were also lower while for first years feeding on food within dung, the levels were not as low as for subsoil feeding. Food within dung is easy to find unlike cryptic, sub-soil food.

Young choughs which were still with their parents had higher swallow rates when feeding on dung than while feeding on sub-soil food. They also spent less time begging, had a lower rate of parental feeding, spent more time feeding, and had higher swallow rates while feeding on dung.

5. AGE OF FIRST BREEDING.

5.1 INTRODUCTION.

It has already been mentioned in the thesis introduction (Section 1.2.4) that there are few data on the age of first breeding in choughs. Holyoak (1972) suggested that, if choughs were similar to other corvids, the age of first breeding would be three. Roberts (1985) found that choughs on Bardsey Island did not in general breed before the age of four and that this was possibly related to a dense population and competition for the relatively few suitable nest sites and territories. Choughs are sedentary and do not move long distances, presumably due to their specialised habitat and food requirements which are influenced by climate (Monaghan *et al.* 1989, C.R. MacKay pers. comm.). Therefore, choughs are restricted in their ability to move to other areas to breed and thus must remain within the non-breeding population until they can gain access to a territory.

The correlation between age of first breeding and annual survival rate has been noted by several authors (Sutherland *et al.* [1986], and Saether [1988]). For a population to remain stable, several strategies may exist. Species with high annual mortality may produce more young or may breed at an earlier age. Birds which have high annual survival rates may produce fewer young, breed intermittently or breed at a later age (Horn & Rubenstein 1978).

Choughs on Islay have a fairly low annual mortality - 26 % in the second year, and a maximum first year mortality rate of 29% (Monaghan *et al.* 1989). Thus, approximately 50% of fledged choughs survive the first two years of life. This means that there is a large number of *potential* breeding choughs in the population

as choughs are capable of breeding at two years old (see below). The age structure of the breeding population (using observations of colour-ringed birds) can give a clearer picture of the age of recruitment into the breeding population and can also be used as a comparison with chough populations in other areas.

Therefore the proportion of the different age classes in the colour-ringed breeding population are examined along with the first age of breeding for different sexes and ages.

5.2 METHODS.

Data used in the analyses are for colour-ringed choughs of known age which were known to reach the egg laying stage. The decision to use only those birds which had laid eggs differentiates them from prospecting birds or birds which built nests but did not breed. Data are included for birds from one cohort which were known to breed in subsequent years. Thus, results are a combination of data over several years (1985 - 1988) although at the time of this analysis complete data on breeding birds were not available and as such the results should be seen as a preliminary analysis which should be analysed further when data become available as more colour-ringed birds enter the breeding population.

5.3 RESULTS

There were 28 colour-ringed choughs of known age and sex. Sexing was carried out following observations by Holyoak (1972), Goodwin (1976) and from personal observation that females alone incubate.

One colour-ringed male was excluded from the analyses as it took over at a nest site where the breeding male was found dead and continued to successfully raise

the brood with the resident widowed female (C.R. MacKay pers. comm.).

Table 5.2.1 shows the numbers and percentage of male and female first time breeders which were either second, third or fourth year and older. Around 72% of female first time breeders were second years with only 9% being four years old or over. First time breeding males of three years accounted for 50% of the first time breeders. Whereas only 9% of female first time breeders were four or older, 25% of male first time breeders were four or older.

Table 5.2.1 The numbers (and percentages) of male and female colour-ringed first time breeding choughs in each age clase.

AGE	NUMBER OF FEMALE FIRST TIME BREEDERS	NUMBER OF MALE FIRST TIME BREEDERS
2nd	2 (18.2)	2 (25)
3rd	8 (72.7)	4 (50)
4th & older	1 (9.1)	2 (25)
	N = 11	N = 8

6. GENERAL DISCUSSION.

The family Corvidae has a wide diversity of social systems ranging from solitary species to species which display high levels of communal or cooperative breeding structure.

Many corvid species have structured non-breeding populations but the degree of sociality when breeding varies from species to species: jackdaws may live in a highly structured social system (Lorenz 1952, Roell 1978); magpies tend to be more solitary breeders but show interesting social behaviour in mass displays thought to be related to territory acquisition, (Vines 1981, Birkhead & Clarkson 1985, Birkhead *et al.* 1986, Eden 1989); crows may be territorial during the breeding season but flock with non-breeding crows at other times of the year (Loman 1985), although Charles (1972) and Spray (1978) found that breeders remained territorial throughout the year. Rooks nest communally and also show a high degree of social organisation at communal roosts (Swingland 1977).

Certain species of New World corvids, however, such as the pinon jay *Gymnorhincus cyanocephalus* (Balda 1971), mexican jay *Aphelocoma ultramarina* (Brown 1963) and Florida scrub jay *Aphelocoma coerulescens* (Woolfenden 1975) have taken sociality, both within and outwith the breeding season, a step further and show strong family associations and a social structure, the basis of which is the extended family.

The results of this study show that non-breeding choughs have a defined social structure and, unlike non-breeders of other species which were described by such

authors as Wynne-Edwards (1962) and Lack (1968), do not lead "a random, wandering kind of existence" (Smith 1984). Previous studies of the chough have dealt with food and feeding habitat, breeding success and mortality (see Section 1.2.6). Little attention had been paid to non-breeders in the population. Any comments on non-breeding flocks were restricted to anecdotal comments about the numbers and locations of encountered roosting or feeding flocks. The only one detailed work on non-breeding chough behaviour was by Warnes (1983a), although her work was restricted by the lack of colour-ringed choughs in the population on Islay at that time. The increase in the numbers of colour-ringed choughs in that population has now allowed for more detailed work on the movements and behaviour of individuals of known age

The high proportion of non-breeding birds in the population is a feature of all chough populations that have been studied in detail, and is similar to several other corvid species in Britain. Magpie populations contain between 20% and 40% non-breeders (Baeyens 1981, Vines 1981, Buitron 1982 and Birkhead *et al.* 1986). Loman (1985) found that in hooded crows, the majority had not become territorial or begun to breed at three years old. This implies that there were a large number of non-breeders in the population, since annual survival was 73% for these non-breeders after their first year of life. Magpies tend, however to breed at an earlier age than choughs, with the majority of the non- breeding population composed mostly of first years with a smaller proportion of second years (Birkhead *et al.* 1986, Eden 1989). The fact that chough non-breeding populations contain higher proportions of older birds may be related to their to their higher survival after fledging (83% of chough survive the first three months after fledging, compared to 36% of magpies over approximately the same period in magpies [Birkhead *et al.* 1986]). Choughs also have a higher survival rate than jackdaws which have a survival rate of 62% in their first year, (Holyoak 1971). Approximately 72% of choughs which fledge survive the first year. A positive correlation between survival rate and age of first breeding has

been found over a range of bird species (Saether 1988), but this may be an inevitable consequence of a stable population size (Sutherland *et al.* 1986).

As there is high annual survival and low dispersal combined with a late age of first breeding in choughs, one might expect a relatively well developed social organisation among birds prior to breeding age. Communal roosts and flock feeding could therefore be a consequence of the above factors.

The studies of the communal roosts of choughs on Islay showed them to be highly structured systems maintained by age-related dominance. This agrees with other studies of avian species which form regular roosts; red-winged blackbirds (Weatherhead & Hoysak 1984), rooks (Swingland 1977), and starlings (Summers *et al* 1987). These species (including the chough) are all social foragers and the advantages of roosting together may not only be a predator avoidance mechanism but may also be related to increasing foraging efficiency, either through local enhancement (Crook 1965, Lack 1968) of by the possible use of roosts as "information centres" (Ward & Zahavi 1973, Weatherhead 1983). For species which feed on ephemeral patchy food this may be one of the major advantages of roosting communally.

As choughs seem to show some form of "information transfer" (using the term with caution as the exact mechanism of information transfer is open to question), it may be important for any reintroduction programme (such as is proposed for Cornwall) to ensure that there are suitable roost sites near feeding areas (since choughs do not generally travel far between feeding and roosting sites. Many of the benefits of communal roosting (including information transfer) will increase with increase in roost size, but roosts may be limited to the size that can be sustained by the surrounding food availability.

As there is movement of choughs to other feeding and roosting sites, especially over the winter period when food availability may be at its lowest, any conservation planning must ensure that choughs are able to find alternative roosts and feeding areas, especially during the winter months if a high level of food availability cannot be guaranteed. The birds which tend to move are mostly young birds which are subsequently found in flocks which contain high proportions of young birds. This has also been observed in rooks (Dunnet *et al.* 1969), starlings (Henty 1989) and marsh tits (Nilsson & Smith 1988). This movement of young, subordinate birds may be due either to older dominant individuals excluding them from certain areas, the voluntary leaving of young birds for reasons unknown or the fact that these birds may congregate on easily accessible food sources (such as the tendency for young starlings to be found feeding in cherry orchards and on dung where food is easily accessible, whereas adults specialised in sub-soil feeding [Stevens 1985]). Young choughs, feeding on dung, achieve similar feeding rates to adults, and could easily gain access to food items. However, they may have to move to another area where there are fewer older, dominant birds. Differences in the food requirements of young, especially those young newly fledged, may exist, as their priorities may differ from those of adults. Food types will differ in their energetic values and protein content, and therefore there may be differences in the quality of food taken by choughs of different age or status. This would need further investigation as this was outwith the bounds of this study. Even though young choughs may have higher feeding rates when feeding on food within dung, older birds may be obtaining food of higher energetic and protein content from less easily accessible food types.

Older choughs which had yet to move from non-breeding flocks to breeding territories tended to remain at one roost with less movement than young choughs. The residency of older birds within one area may allow them to benefit from knowledge of the feeding area surrounding the roost. Caccamise & Morrison (1986

& 1988) found that starlings tended to use several roosts but return to the same feeding area during the day (i.e. they were more faithful to feeding areas ["diurnal activity centres"] than to night roosts) and the choice of roost was more closely related to the birds' exploitation of short term food sources away from their regular feeding area. Choughs, in comparison, tend to be faithful to roost sites, and the fact that they do not travel far to feed suggests that food availability close to the roost is high and consistent for long enough (although actual sites and types of food may change) to allow them to remain at one roost for relatively long periods.

As choughs are opportunistic feeders and quickly take advantage of newly accessible food (such as grain in stubble, sub-soil invertebrates after silage and hay cut and the use of areas where livestock are fed [pers. obs.]), one would predict that roosting sites should be close to areas where a range of food types becomes seasonally available. The fact that one roost (Roost 1) was in use over the whole year while the others were used on a temporary basis suggests that a factor in the choice of roost site may be related to the availability of food round the roost. Young choughs may be forced to move to other roosts especially during the winter to take advantage of short lived food sources whereas older choughs are able, either through higher dominance status or knowledge of an area to make use of the more limited food availability around one roost. This is, however a circular argument. Older choughs may be resident and dominant because of their better foraging ability or may have a greater foraging ability because they are resident and dominant!

Young choughs with their parents are able to feed at a higher rate while feeding on dung than when feeding with their parents in areas such as silage cut fields. Higher feeding rates however do not necessarily indicate higher intake for this will depend on the prey size and also its nutritional quality. Further work on the availability of such easily accessible food sources, especially for newly fledged

choughs, may tell whether the survival of young choughs is increased if dung density is high.

The majority of the young choughs that join the feeding and roosting non-breeding flocks and roost with them soon after fledging arrive with their parents and remain in family groups within the non-breeding flocks for up to six weeks after fledging. Some of these families travel up to 15 km from their breeding site. Observations on three families in 1987 showed that in two cases the families arrived to join the non-breeding flock which was associated with Roost 1. They then returned to their nest sites within two to three days. For one family which originated from a breeding site 10 km away, this process was repeated three times with daily visits to the non-breeding flock although returning each evening to the nest to roost. Eventually the young remained with the non-breeding flock while the parents returned to the breeding territory. In the case of another family, the parents and three young travelled 15 km to the non-breeding flock then returned to the breeding territory with two of the young after spending one night at the communal roost. The remaining newly fledged chough (fledged for approximately 10 days) was eventually found 18 km away from its natal site and in the company of another family with fledged young. One young chough remained with its parents and roosted at the nest site until late winter/early spring, when it finally travelled 15 km to join a non-breeding flock.

The reasons for the variation in time taken for young choughs to leave their natal territories, and the movement back and forth of families to non-breeding flocks over considerable distances on a daily basis, are unknown. Food availability for parents and young on the breeding territory may be an important factor. It may be that some families are forced to join the non-breeding flocks at an early stage due to the food supply on the breeding territory not being sufficient to sustain the

entire family. In the case of the one young chough which remained in the natal area with its parents, food availability may have been high enough and for long enough to sustain both parents and one young. (The family groups which moved back and forth from the breeding site had 3 and 4 fledged offspring).

The majority of choughs do not breed until at least three years of age although some hold territories in their second year. In the period between fledging and breeding they may form several close associations before breeding (pers. obs.). This has been observed by Roberts (1985) where he noted that first and second year choughs went through pair-bonding and pairing activities such as allopreening and mutual feeding. However, these birds were not all paired but "clearly promiscuous" with birds which seemed to be paired being seen shortly after with another bird. Although choughs may form associations in their first year, data available suggest that the majority of chough on Islay breed for the first time at three years old.

Any reintroduction of choughs to other areas of Britain will probably have to rely on captive breeding programmes to provide the basis for the reintroduced population. Successful captive breeding may depend on allowing the young choughs to form their own association while within a group rather than by placing two adult choughs together in the expectation that they will breed. The promiscuous nature of these young choughs may be a mechanism that allows them to chose as suitable a mate as possible, so that the breeding success of these natural pairs may be higher than a pair which have been placed together in a captive situation. Experimental studies of canvasback ducks (*Aythya valisineria*) have shown that birds isolated as breeding pairs produced no eggs if the two birds had been artificially chosen at random but bred successfully if they had been allowed to pair naturally within a captive flock (Bluhm in Metcalfe & Monaghan 1987). The choice of a suitable mate may be another function of communal roosting and feeding for non-breeding choughs as it may facilitate the mixing of choughs from a wide area over which

nest sites are thinly dispersed.

Future work should look at the habitat choices and food requirements of non-breeding choughs in relation to their status and age. The foraging strategies used by young choughs would presumably be related to the availability of suitable habitats and food sources and these factors should be investigated. Habitat choice of young choughs, and in particular those that have newly fledged, should be investigated in relation to their survival. It may be possible to look at the reasons for the movements of young choughs if they are related to competition for food from older birds. Electronic balances could be placed in roosts and regular measurements of weights of birds taken to assess the body condition in relation to age. The movement of young choughs to new areas may be triggered by weight loss and if possible, weight measurements could be taken from these young choughs after they have moved. It would also be of interest to compare these with the weights of those young choughs that remained when the others departed, since these remaining young may be ones which are better foragers, able to compete with older dominant choughs. For all non-breeders, the ability to enter the breeding population may be related to their foraging success and their ability to therefore reach a body condition level allowing them to breed. Therefore, the habitat requirements of all non-breeders should be investigated to allow for the conservation of suitable areas for these future members of the breeding population.

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Appendix 1. Mean monthly flocksize and corrected roost numbers (± 1 s.e.) for each of chough at Roost 1.

1985			COHORT				
MONTH	N	FLOCKSIZE	1983	1984	1985	1986	1987
MAR	11	70.9±3.6	25.6±1.6	27.6±2.3	--	--	--
APR	8	76.9±4.8	21.1±1.6	30.4±4.2	--	--	--
MAY	3	100.0±0.0	20.2±1.0	50.2±3.6	--	--	--
JUN	9	89.4±4.3	27.5±1.6	20.1±3.4	--	--	--
JUL	8	123.7±1.8	30.4±1.3	51.2±2.3	16.2±2.1	--	--
AUG	0	--	--	--	--	--	--
SEP	13	98.5±1.5	24.6±1.6	34.1±1.8	13.6±1.6	--	--
OCT	0	--	--	--	--	--	--
NOV	0	--	--	--	--	--	--
DEC	2	72.5±2.5	17.6±1.6	14.3±6.5	6.4±3.2	--	--

Appendix 1. Mean monthly flocksize and corrected roost numbers (± 1 s.e.) for each cohort of chough at Roost 1.

1986			COHORT				
MONTH	N	FLOCKSIZE	1983	1984	1985	1986	1987
JAN	1	120.0 ± 0.0	22.4 ± 0.0	18.2 ± 0.0	6.4 ± 0.0	--	--
FEB	17	115.5 ± 1.6	22.1 ± 1.3	35.1 ± 2.6	15.0 ± 1.0	--	--
MAR	16	118.3 ± 1.6	21.1 ± 1.3	42.6 ± 2.1	19.2 ± 1.0	--	--
APR	8	100.0 ± 2.1	6.1 ± 1.3	31.2 ± 1.8	19.2 ± 1.1	--	--
MAY	15	97.3 ± 1.4	12.2 ± 1.0	38.7 ± 1.6	24.8 ± 1.1	--	--
JUN	19	98.4 ± 2.2	14.4 ± 0.6	30.7 ± 1.3	20.6 ± 0.8	--	--
JUL	19	106.6 ± 1.6	17.3 ± 1.0	33.0 ± 1.6	20.3 ± 1.1	7.0 ± 1.2	--
AUG	12	125.4 ± 1.7	21.1 ± 1.9	37.2 ± 1.0	27.5 ± 0.8	19.7 ± 1.9	--
SEP	8	114.4 ± 2.4	13.4 ± 1.3	26.3 ± 2.3	14.2 ± 1.0	24.2 ± 1.9	--
OCT	0	--	--	--	--	--	--
NOV	0	--	--	--	--	--	--
DEC	0	--	--	--	--	--	--

Appendix 1. Mean monthly flocksize and corrected roost numbers (± 1 s. for each cohort of chough at Roost 1.

1987			COHORT				
MONTH	N	FLOCKSIZE	1983	1984	1985	1986	1987
JAN	2	72.5 ± 2.5	11.2 ± 4.8	22.1 ± 1.3	6.4 ± 0.0	0.0 ± 0.0	--
FEB	6	73.3 ± 1.7	16.0 ± 1.6	28.6 ± 3.1	8.8 ± 0.8	0.7 ± 0.5	--
MAR	10	66.3 ± 1.5	11.2 ± 1.3	15.9 ± 1.3	13.8 ± 1.3	1.9 ± 0.5	--
APR	1	60.0 ± 0.0	6.4 ± 0.0	5.2 ± 0.0	16.0 ± 0.0	2.4 ± 0.0	--
MAY	9	55.2 ± 1.9	6.4 ± 0.6	17.2 ± 0.5	19.0 ± 0.5	13.7 ± 0.5	--
JUN	6	55.8 ± 2.0	5.8 ± 0.6	13.5 ± 0.8	14.1 ± 1.4	12.7 ± 1.9	--
JUL	20	95.2 ± 2.1	13.8 ± 1.0	19.5 ± 0.5	19.0 ± 1.0	34.6 ± 1.9	9.2 ± 1.2
AUG	11	67.3 ± 4.0	9.0 ± 1.0	12.2 ± 0.8	14.6 ± 1.1	13.9 ± 2.4	11.6 ± 1.0
SEP	8	45.4 ± 1.4	5.1 ± 0.6	12.0 ± 0.8	9.6 ± 0.3	5.3 ± 0.5	5.4 ± 1.2
OCT	0	--	--	--	--	--	--
NOV	7	35.4 ± 0.4	6.7 ± 0.3	12.0 ± 0.8	7.0 ± 0.6	3.1 ± 1.0	0.0 ± 0.0
DEC	5	33.0 ± 1.2	8.3 ± 1.3	11.4 ± 1.3	6.1 ± 0.6	3.4 ± 1.2	0.0 ± 0.0
1988							
JAN	13	36.8 ± 0.7	8.3 ± 0.6	15.1 ± 0.5	6.4 ± 0.3	2.4 ± 0.5	0.0 ± 0.0
FEB	4	39.5 ± 0.5	8.6 ± 0.6	18.2 ± 0.0	6.7 ± 0.3	1.7 ± 0.5	0.0 ± 0.0

Appendix 2. Breakdown of arrivals and departures from Roost 1 of colour-ringed choughsbirds (for months with 3 and more roost observation nights.)

1986 ARRIVALS * denotes fledged

MONTH	AGE	BREEDING/NESTING ATTEMPT	TERRITORY	OTHER FLOCK/ ROOST	UNKNOWN
FEB	1st	--	--	--	7
	2nd	--	--	--	4
	3rd	--	--	--	5
MAR	1st	--	--	--	--
	2nd	--	--	--	--
	3rd	--	--	--	1
APR	1st	--	--	3	--
	2nd	--	--	--	--
	3rd	--	--	--	1
MAY	1st	--	--	--	7
	2nd	--	--	--	5
	3rd	2	--	--	1
JUN	1st	--	--	--	--
	2nd	--	--	--	--
	3rd	1	--	--	1
JUL	1st	--	--	--	9*
	2nd	--	--	--	--
	3rd	--	--	--	--
	4th	1	--	--	--
AUG	1st	--	--	--	11*
	2nd	--	--	--	--
	3rd	--	--	--	--
	4th	--	--	--	--
SEP	1st	--	--	--	3
	2nd	--	--	--	--
	3rd	--	--	--	--
	4th	--	--	--	--
OCT/ NOV/ DEC/ JAN '87	1st	--	--	--	--
	2nd	--	--	--	--
	3rd	--	--	--	2
	4th	--	--	--	2

Appendix 2. cont. Breakdown of arrivals and departures from Roost 1 of colour-ringed choughs (for months with 3 and more roost observation nights.)

1987 ARRIVALS * denotes fledged

MONTH	AGE	BREEDING/NESTING ATTEMPT	TERRITORY	OTHER FLOCK/ ROOST	UNKNOWN
FEB	1st	--	--	--	--
	2nd	--	--	2	--
	3rd	--	--	1	3
	4th	--	--	--	1
MAR	1st	--	--	2	1
	2nd	--	--	5	1
	3rd	--	--	--	--
	4th	--	--	--	--
APR/	1st	--	--	3	--
MAY	2nd	--	1	3	3
	3rd	--	1	2	3
	4th	--	1	--	--
JUN	1st	--	--	6	--
	2nd	--	1	--	--
	3rd	--	--	--	1
	4th	--	1	--	--
JUL	1st	--	--	--	16*
	2nd	--	--	--	11
	3rd	1	1	--	4
	4th	2	--	--	2
	5th	5	--	--	--
AUG	1st	--	--	4	--
	2nd	--	--	--	--
	3rd	--	--	--	--
	4th	--	1	--	--
	5th	--	--	--	--
SEP	1st	--	--	--	--
	2nd	--	--	--	--
	3rd	--	--	--	--
	4th	--	--	--	--
	5th	--	--	--	--
OCT/	1st	--	--	--	--
NOV	2nd	--	--	--	--
	3rd	--	--	2	--
	4th	--	--	--	--
	5th	--	1	--	--
DEC	1st	--	--	--	--
	2nd	--	--	--	--
	3rd	--	--	1	--
	4th	--	--	--	--
	5th	--	--	--	1

Appendix 2. cont. Breakdown of arrivals and departures from Roost 1 of colour-ringed choughs (for months with 3 and more roost observation nights.)

1988 ARRIVALS

MONTH	AGE	BREEDING/NESTING ATTEMPT	TERRITORY	OTHER FLOCK/ ROOST	UNKNOWN
JAN	1st	--	--	--	--
	2nd	--	--	--	--
	3rd	--	1	2	--
	4th	--	--	--	3
	5th	--	--	--	--
FEB	1st	--	--	--	--
	2nd	--	--	--	--
	3rd	--	--	--	--
	4th	--	--	--	--
	5th	--	--	--	--

Appendix 2. cont. Breakdown of arrivals and departures from Roost 1 of colour-ringed choughs (for months with 3 and more roost observation nights.)

1986 DEPARTURES

MONTH	AGE	BREEDING/NESTING TERRITORY ATTEMPT		OTHER FLOCK/ ROOST	UNKNOWN	
					ALIVE	NOT SEEN AGAIN
FEB	1st	--	--	2	2	--
	2nd	--	--	--	--	--
	3rd	--	--	--	1	--
MAR	1st	--	--	--	3	1
	2nd	--	1	--	2	--
	3rd	4	--	--	2	--
APR	1st	--	--	--	--	--
	2nd	--	--	--	5	2
	3rd	1	--	--	--	1
MAY	1st	--	--	--	--	--
	2nd	--	--	--	1	--
	3rd	--	--	--	1	--
JUN	1st	--	--	--	--	--
	2nd	--	--	--	--	--
	3rd	--	--	--	--	--
JUL	1st	--	--	--	--	--
	2nd	--	--	--	--	--
	3rd	--	--	--	--	--
	4th	--	--	--	--	--
AUG	1st	--	--	3	--	1
	2nd	--	--	3	--	--
	3rd	--	--	--	--	--
	4th	--	2	--	1	--
SEP	1st	--	--	1	2	5
	2nd	--	1	5	1	1
	3rd	--	--	5	4	--
	4th	--	--	--	1	--
OCT/ NOV/ DEC/ JAN'87	1st	--	--	3	--	8
	2nd	--	--	2	--	3
	3rd	--	--	4	--	--
	4th	2	--	--	--	--

Appendix 2. cont. Breakdown of arrivals and departures from Roost 1 of colour-ringed choughs (for months with 3 and more roost observation nights.)

1987 DEPARTURES

MONTH	AGE	BREEDING/NESTING ATTEMPT	TERRITORY	OTHER FLOCK/ ROOST	UNKNOWN	
					ALIVE NOT SEEN	AGAIN
FEB	1st	--	--	--	--	--
	2nd	--	--	1	--	--
	3rd	1	--	1	1	1
	4th	--	--	--	--	--
MAR	1st	--	--	1	--	--
	2nd	--	--	--	--	--
	3rd	2	1	--	3	--
	4th	1	2	--	1	--
APR/	1st	--	--	--	--	--
MAY	2nd	--	1	--	5	--
	3rd	1	--	--	4	--
	4th	1	--	--	--	--
JUN	1st	--	--	--	--	--
	2nd	--	--	--	2	1
	3rd	--	--	--	1	--
	4th	--	--	--	--	--
JUL	1st	--	--	3	--	3
	2nd	--	--	8	--	1
	3rd	--	2	1	--	--
	4th	--	2	--	1	--
	5th	--	3	--	--	--
AUG	1st	--	--	3	--	4
	2nd	--	--	11	--	--
	3rd	--	--	3	1	--
	4th	--	--	--	3	--
	5th	--	1	--	2	--
SEP	1st	--	--	3	1	4
	2nd	--	--	--	--	--
	3rd	--	--	5	--	1
	4th	--	--	1	--	--
	5th	--	1	--	--	--
OCT/	1st	--	--	--	--	--
NOV	2nd	--	--	--	--	--
	3rd	--	--	--	--	--
	4th	--	--	3	--	--
	5th	--	--	--	--	--
DEC	1st	--	--	1	--	--
	2nd	--	--	--	--	--
	3rd	--	--	--	--	--
	4th	--	--	--	--	--
	5th	--	--	--	--	--

Appendix 2. cont. Breakdown of arrivals and departures from Roost 1 of colour-ringed choughs (for months with 3 and more roost observation nights.)

1988 DEPARTURES

MONTH	AGE	BREEDING/NESTING TERRITORY ATTEMPT	OTHER FLOCK/ ROOST	UNKNOWN	
				ALIVE	NOT SEEN AGAIN
JAN	1st	--	--	--	--
	2nd	--	--	--	--
	3rd	--	2	--	--
	4th	--	--	2	--
	5th	--	--	--	--
FEB	1st	--	--	--	--
	2nd	--	--	--	--
	3rd	--	1	--	--
	4th	--	--	--	--
	5th	--	--	--	--

Appendix 3. Details of surveys carried out in areas corresponding to three roosts, Roosts 1,2 & 3.

ROOST 1

MONTHS	TIME	NO. COLOUR-RINGED CHOUGHS AT ROOST	PROPORTION FOUND ON SURVEY
Feb. '86	am.	32	0.625
Feb. '86	am.	36	0.750
Feb. '86	pm.	48	0.625
Mar. '86	pm.	45	0.422
Mar. '86	am.	41	0.731
Apr. '86	am.	38	0.736
Apr. '86	pm.	30	0.866
May. '86	am.	47	0.893
May. '86	pm.	48	0.708
Jun. '86	am.	48	0.604
Jun. '86	pm.	41	0.804
Jul. '86	am.	41	0.634
Jul. '86	pm.	47	0.595
Aug. '86	am.	52	0.769
Aug. '86	pm.	57	0.719
Sep. '86	am.	52	0.634
Sep. '86	pm.	37	0.864
Nov. '86	am.	35	0.885
Jan. '87	pm.	28	0.821
Feb. '87	pm.	27	0.888
Feb. '87	am.	25	0.960
Mar. '87	pm.	26	0.769
Mar. '87	am.	22	0.818
Mar. '87	pm.	24	0.833
May. '87	am.	32	0.875
May. '87	pm.	32	0.843
Jun. '87	am.	29	0.896
Jun. '87	pm.	30	0.700
Jul. '87	am.	66	0.742
Jul. '87	am.	58	0.689
Jul. '87	pm.	65	0.646
Aug '87	pm.	50	0.620
Aug. '87	am.	26	0.884
Sep. '87	am.	24	0.791
Sep. '87	pm.	23	0.869
Nov. '87	am.	16	0.750
Jan. '88	am.	13	1.000

mean proportion of roosting colour-ringed choughs found on surveys= 0.76 $\pm$ 0.02 s.e.

Appendix 3 cont. Details of surveys carried out in areas corresponding to three roosts, Roosts 1, 2 & 3.

ROOST 2

MONTHS	TIME	NO. RINGED BIRDS AT	PROPORTION FOUND ON SURVEY
Aug. '86	am.	18	1.000
Aug. '86	pm.	19	0.894
Sep. '86	am.	23	0.956
Sep. '86	pm.	29	0.931
Nov. '86	am.	28	0.964
Jan. '87	pm.	23	1.000
Feb. '87	am.	21	0.904
Feb. '87	am.	23	0.826
Mar. '87	am.	23	0.913
Mar. '87	am.	23	0.869
Aug '87	pm.	10	0.900
Sep. '87	pm.	21	0.714
Nov. '87	am.	20	0.900
Nov. '87	am.	21	0.666
Dec. '87	pm.	11	0.363
Jan. '88	pm.	12	0.583

mean proportion of roosting colour-ringed choughs found on surveys= 0.84 $\pm$ 0.04 s.e.

ROOST 3

MONTHS	TIME	NO. RINGED BIRDS AT	PROPORTION FOUND ON SURVEY
ROOST			
Jan. '87	am.	14	0.642
Feb. '87	am.	11	0.727
Feb. '87	pm.	8	0.750
Mar. '87	am.	7	0.714
May '87	am.	18	0.888
May '87	pm.	17	0.941
Jun. '87	am.	16	0.812
Jun. '87	pm.	16	0.812
Aug. '87	am.	19	0.842
Nov. '87	am.	21	0.714
Jan. '88	am.	19	0.894

mean proportion of roosting colour-ringed choughs found on surveys= 0.79 $\pm$ 0.03 s.e.

Appendix 4. Mean ± s.e. proportions (arcsine transformed) of colour-ringed choughs of four age classes in core area 1 (choughs using Roost 1) in different flock sizes. Data shown for three seasons: spring, summer & winter. Sample sizes in brackets.

FLOCK SIZE	AGE 1st mean	1st s.e.	2nd mean	2nd s.e.	3rd mean	3rd s.e.	4th/5th mean	4th/5th s.e.
SPRING.								
1	0.59	0.12 (12)	0.15	0.10 (12)	0.15	0.10 (12)	0.00	0.00 (4)
2	0.15	0.06 (35)	0.20	0.05 (35)	0.41	0.06 (35)	0.28	0.09 (16)
3-5	0.48	0.05 (56)	0.25	0.04 (56)	0.15	0.04 (56)	0.02	0.02 (18)
6-10	0.45	0.04 (58)	0.35	0.04 (58)	0.09	0.02 (58)	0.06	0.03 (19)
11-15	0.37	0.05 (44)	0.40	0.04 (44)	0.12	0.03 (44)	0.11	0.03 (23)
16-20	0.28	0.04 (26)	0.39	0.03 (26)	0.23	0.03 (26)	0.13	0.03 (21)
21-40	0.23	0.01 (106)	0.43	0.13 (106)	0.27	0.01 (106)	0.17	0.01 (80)
41-60	0.29	0.01 (62)	0.41	0.01 (62)	0.29	0.01 (62)	0.16	0.01 (54)
> 60	0.29	0.06 (8)	0.45	0.03 (8)	0.24	0.04 (8)	0.27	-- (1)
SUMMER.								
1	0.29	0.06 (45)	0.16	0.05 (45)	0.29	0.06 (45)	0.12	0.04 (51)
2	0.06	0.02 (148)	0.07	0.02 (148	0.34	0.03 (148)	0.33	0.03 (189)
3-5	0.39	0.03 (185)	0.12	0.02 (185)	0.22	0.02 (185)	0.13	0.02 (241)
6-10	0.29	0.04 (77)	0.24	0.03 (77)	0.23	0.03 (77)	0.12	0.02 (115)
11-15	0.29	0.04 (72)	0.24	0.02 (72)	0.24	0.02 (72)	0.14	0.01 (118)
16-20	0.24	0.03 (48)	0.25	0.03 (48	0.27	0.02 (48)	0.16	0.02 (86)
21-40	0.20	0.02 (79)	0.29	0.02 (79)	0.31	0.01 (79)	0.19	0.01 (135)
41-60	0.15	0.02 (46)	0.33	0.02 (46)	0.33	0.01 (46)	0.21	0.01 (82)
> 60	0.17	0.02 (49)	0.34	0.01 (49)	0.33	0.01 (49)	0.20	0.01 (86)
WINTER.								
1	0.37	0.10 (19)	0.14	0.08 (19)	0.23	0.09 (19)	0.16	0.09 (16)
2	0.19	0.05 (46)	0.06	0.03 (46)	0.20	0.04 (46)	0.34	0.04 (59)
3-5	0.19	0.02 (48)	0.16	0.04 (48)	0.16	0.04 (48)	0.28	0.07 (28)
6-10	0.29	0.06 (45)	0.13	0.04 (45)	0.25	0.04 (45)	0.11	0.02 (168)
11-15	0.21	0.05 (30)	0.20	0.03 (30)	0.32	0.04 (30)	0.29	0.05 (24)
16-20	0.26	0.06 (21)	0.26	0.04 (21)	0.29	0.04 (21)	0.23	0.04 (17)
21-40	0.11	0.01 (69)	0.31	0.02 (69)	0.37	0.02 (69)	0.28	0.01 (61)
41-60	0.18	0.04 (18)	0.39	0.03 (18)	0.35	0.02 (18)	0.30	0.02 (7)
> 60	0.20	0.03 (21)	0.43	0.02 (21)	0.33	0.02 (21)	0.27	0.02 (6)

Appendix 4. Mean ± s.e. proportions (arcsine transformed) of colour-ringed choughs of four age classes in core area 2 (choughs using Roost 2) in different flock sizes. Data shown for three seasons: spring, summer & winter. Sample sizes in brackets.

FLOCK SIZE	AGE 1st mean	1st s.e.		2nd mean	2nd s.e.		3rd mean	3rd s.e.		4th/5th mean	4th/5th s.e.	
SPRING.												
1	0.00	--	(1)	0.00	--	(1)	0.88	--	(1)	0.00	--	(1)
2	0.59	0.29	(3)	0.00	0.00	(3)	0.29	0.03	(3)	0.00	0.00	(3)
3-5	0.46	0.26	(3)	0.09	0.09	(3)	0.29	0.29	(3)	0.09	0.09	(3)
6-10	0.85	0.02	(14)	0.02	0.02	(14)	0.02	0.02	(14)	0.00	0.00	(14)
11-15	0.75	0.03	(9)	0.09	0.03	(9)	0.04	0.01	(9)	0.02	0.02	(9)
16-20	0.70	0.03	(10)	0.18	0.03	(10	0.01	0.01	(10)	0.17	0.17	(10)
> 2	0.66	0.01	(16)	0.20	0.01	(16)	0.06	0.02	(16)	0.05	0.02	(16)
SUMMER.												
1	0.88	0.00	(3)	0.00	0.00	(3)	0.00	0.00	(3)	0.00	0.00	(4)
2	0.34	0.01	(13)	0.00	0.00	(13)	0.14	0.09	(13)	0.24	0.09	(22)
3-5	0.83	0.03	(30)	0.04	0.03	(30)	0.01	0.01	(30)	0.00	0.00	(45)
6-10	0.80	0.04	(30)	0.06	0.03	(30)	0.00	0.00	(30)	0.02	0.01	(38)
11-15	0.71	0.05	(22)	0.12	0.04	(22)	0.06	0.02	(22)	0.02	0.01	(30)
16-20	0.70	0.11	(8)	0.10	0.08	(8)	0.08	0.04	(8)	0.02	0.02	(12)
> 20	0.63	0.04	(3)	0.00	0.00	(3)	0.18	0.01	(3)	0.08	0.05	(6)
WINTER.												
1	0.81	0.07	(12)	0.07	0.07	(12)	0.00	0.00	(12)	0.00	0.00	(14)
2	0.23	0.06	(47)	0.35	0.06	(47)	0.14	0.04	(47)	0.10	0.03	(74)
3-5	0.45	0.05	(51)	0.32	0.05	(51)	0.06	0.02	(51)	0.06	0.02	(73)
6-10	0.33	0.04	(54)	0.41	0.04	(54)	0.11	0.02	(54)	0.06	0.01	(79)
11-15	0.42	0.06	(35)	0.38	0.05	(35)	0.07	0.02	(35)	0.08	0.01	(49)
16-20	0.44	0.08	(13)	0.36	0.06	(13)	0.06	0.03	(13)	0.08	0.02	(17)
21-40	0.56	0.02	(20)	0.24	0.02	(20)	0.11	0.03	(20)	0.10	0.01	(21)
> 40	0.56	0.02	(3)	0.22	0.01	(3)	0.21	0.05	(3)	0.09	0.05	(3)

Appendix 4. Mean ± s.e. proportions (arcsine transformed) of colour-ringed choughs of four age classes in core area 3 (choughs using Roost 3) in different flock sizes. Data shown for three seasons: spring, summer & winter. Sample sizes in brackets.

FLOCK SIZE	AGE 1st mean	1st s.e.	2nd mean	2nd s.e.	3rd mean	3rd s.e.	4th/5th mean	4th/5th s.e.
SPRING.								
1	--		--		--		--	
2	0.44	0.44 (2)	0.44	0.44 (2)	0.00	0.00 (2)	0.00	0.00 (2)
3-5	0.77	0.11 (8)	0.11	0.11 (8)	0.00	0.00 (8)	0.00	0.00 (8)
6-10	0.56	0.12 (11)	0.32	0.12 (11)	0.00	0.00 (11)	0.00	0.00 (11)
11-15	0.88	0.00 (2)	0.00	0.00 (2)	0.00	0.00 (2)	0.00	0.00 (2)
16-20	0.84	0.04 (6)	0.03	0.03 (6)	0.03	0.03 (6)	0.00	0.00 (6)
> 20	0.82	0.07 (8)	0.07	0.07 (8)	0.00	0.00 (8)	0.00	0.00 (8)
SUMMER.								
1	--		--		--		--	
2	0.13	0.13 (7)	0.00	0.00 (7)	0.32	0.01 (7)	0.52	0.13 (7)
3-5	0.80	0.05 (20)	0.01	0.01 (20)	0.06	0.05 (20)	0.02	0.02 (20)
6-10	0.66	0.06 (29)	0.01	0.04 (29)	0.10	0.03 (29)	0.05	0.03 (29)
11-15	0.57	0.09 (11)	0.19	0.06 (11)	0.15	0.05 (11)	0.06	0.03 (11)
16-20	0.37	0.09 (10)	0.24	0.07 (10)	0.26	0.04 (10)	0.21	0.03 (10)
> 20	0.29	0.05 (7)	0.48	0.04 (7)	0.12	0.05 (7)	0.20	0.01 (7)
WINTER.								
1	0.25	0.16 (7)	0.38	0.18 (7)	0.25	0.16 (7)	0.00	0.00 (14)
2	0.44	0.13 (12)	0.18	0.10 (12)	0.11	0.06 (12)	0.07	0.04 (24)
3-5	0.65	0.07 (27)	0.09	0.05 (27)	0.15	0.06 (27)	0.00	0.00 (54)
6-10	0.53	0.08 (23)	0.14	0.05 (23)	0.23	0.06 (23)	0.01	0.00 (46)
11-15	0.23	0.06 (7)	0.27	0.05 (7)	0.42	0.01 (7)	0.06	0.03 (14)
16-20	0.18	0.05 (11)	0.31	0.03 (11)	0.44	0.01 (11)	0.06	0.02 (22)
21-40	0.22	0.06 (10)	0.28	0.05 (10)	0.38	0.02 (10)	0.10	0.03 (20)
> 40	0.30	0.01 (3)	0.20	0.01 (3)	0.41	0.00 (3)	0.14	0.05 (6)